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THE LIVING BIRD

NINETEENTH ANNUAL

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1980-81

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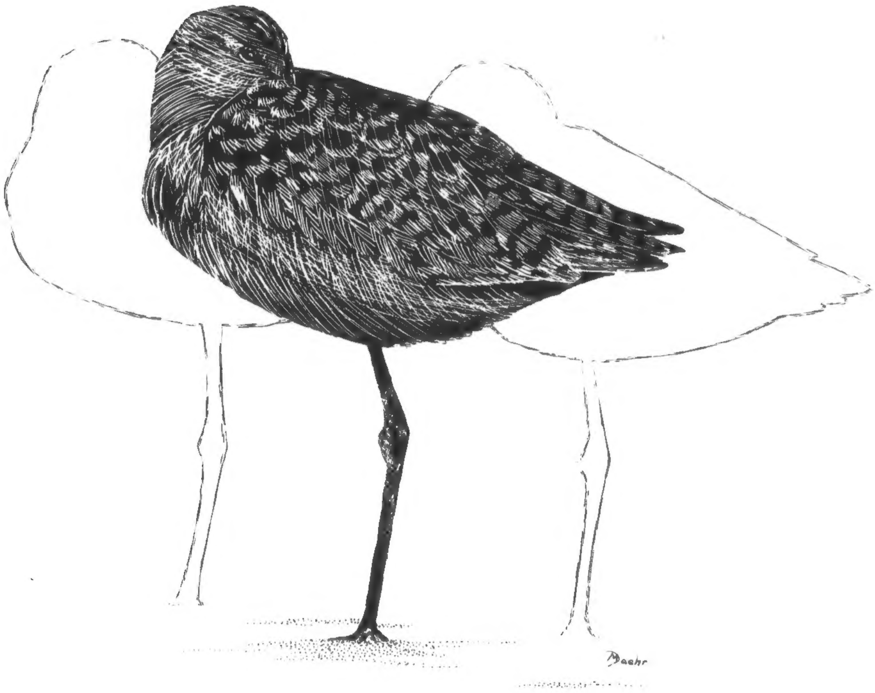

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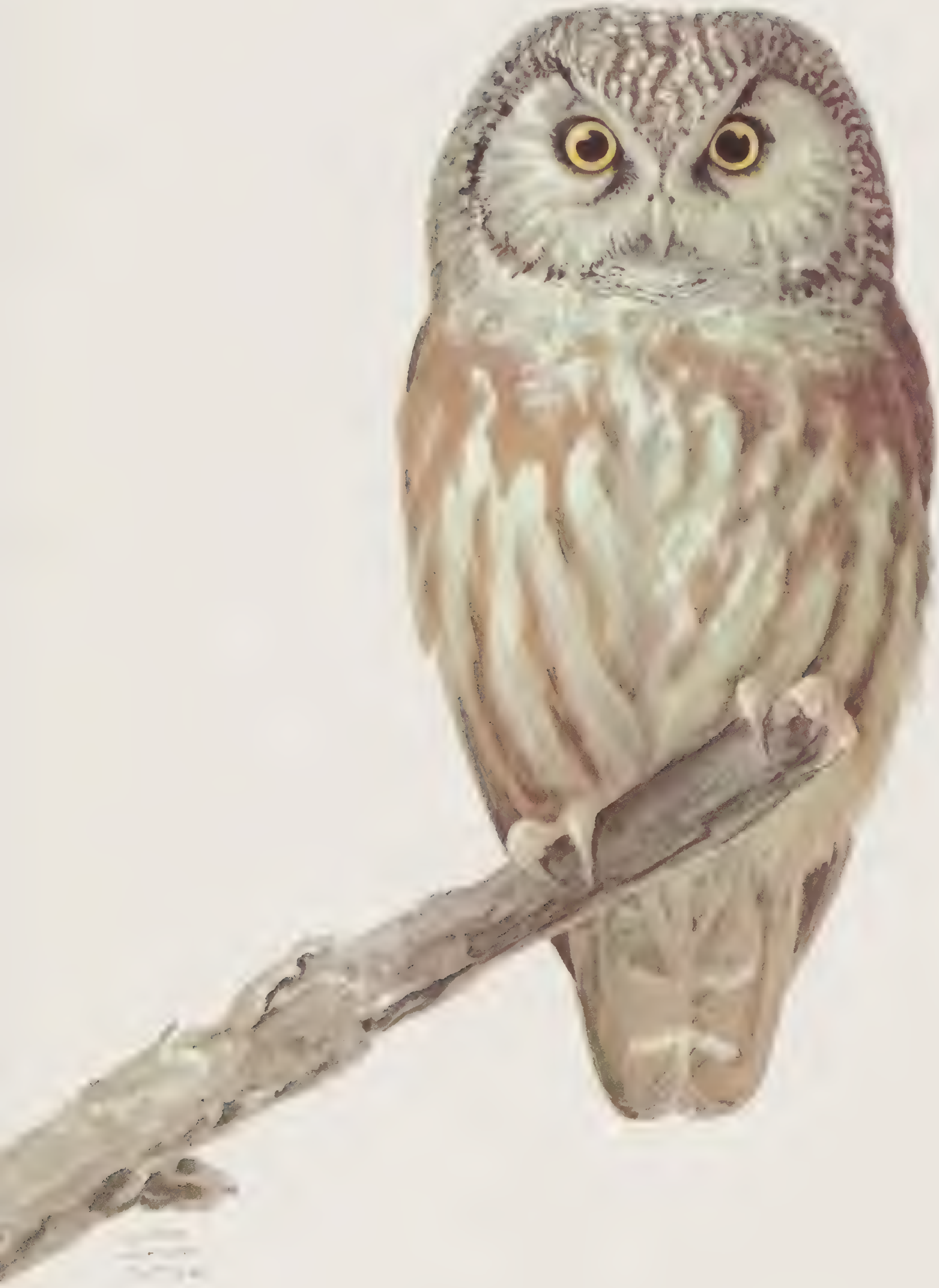

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A BOREAL OWL PORTRAIT

George Miksch Sutton

How fortunate that the not-very-well-known small owl whose scientific name is *Aegolius funereus* has managed to escape being called the Funereal Owl. Fancy having to call any owl with golden eyes *funereal!*

While I was a youth, the bird books all called this species Richardson's Owl, a name based on "*Nyctale Richardsoni*," the binominal bestowed in 1838 by Charles Lucien Bonaparte. Bonaparte was convinced that the American bird was both darker-backed and more heavily streaked with brown on its underparts than its Eurasian counterpart, and described it as a new species, naming it in honor of Sir John Richardson the British naturalist. Today the American form and several Eurasian forms are believed to be one great species, with round-the-pole distribution. The best known of the Old World races is called Tengmalm's Owl in England. The largest and palest of the races is Siberian. Strictly a woodland bird, *Aegolius funereus* ranges well northward, but nowhere beyond tree limit.

Whatever its name, the bird seems to elude mankind most of the time. Although I have been afield in Canadian woodlands for months on end, I have never seen the species there. The fine spruce forests along the Abitibi and Missanabie rivers—as I saw them in 1923 and 1926, respectively — were ideal habitat for the owl, yet I looked and listened for it in vain. W. E. Clyde Todd, whose monumental "Birds of the Labrador Peninsula" (1963; Carnegie Museum and Univ. Toronto Press) is a delight to read, has this to say: "I have repeatedly heard cries at night in the north country which I suspected came from owls of this species, but I have never personally met with it" (p. 451). My comment here is that after a full day of paddling, portaging, skinning specimens, and writing notes I usually slept so soundly that I heard not a thing at night.

It was in Alaska, during World War II, that I had my first look at a live Boreal Owl. I was in uniform at Ladd Field, near Fairbanks, testing survival equipment. On 25 March 1945 word reached me that a "little owl" had been seen along a road skirting Chena Slough, that the bird had seemed "positively stupid," and that a Russian civilian named Alexander Bajkov (a delightful man with sparkling gray eyes) had approached to within five feet and photographed it. Intrigued by every word I could squeeze out of my informants, I begged to be taken to the place at which the owl had been seen.

My guide and I walked about six miles before reaching the "owl spot." The going was easy, for the road had been in use. I could not help wondering whether the "owl tree" pointed out was indeed the right one, for the hundreds of spruces through which the road led all looked alike. At any

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Boreal Owl, *Aegolius funereus*. Painted from life by George Miksch Sutton.

rate, no owl was there. Determined not to give up too easily, we tramped through the deep snow in widening circles . . . and found the owl (or one of the same species) about 200 yards from the road. We might never have seen it had it not flown. It alighted on a birch stub about 15 feet from the ground. Fearful that if it flew again, it would be gone for good, I shot it with the .22 firearm that was part of the standard equipment placed in aircraft. The soft little carcass was lovely, the eyes like precious stones. Nurses and doctors gathered around as I skinned the specimen that evening. Parts of a short-tailed mouse were in its stomach.

Two years later, in Michigan, I again saw a living Boreal Owl. This time the bird was a captive sent to the University of Michigan by Hugo E. Kilpela, a biology teacher in Newberry, a town in Michigan's Upper Peninsula about 300 miles north of Ann Arbor. The owl had been found "napping" in a barn on the Pentland farm near Newberry on 16 March by Melvin Verette, one of Kilpela's students. Melvin caught it after knocking it from its perch on a rope with a "clot of dirt." It seemed to fare well in captivity, but shipment to Ann Arbor was delayed and when the bird reached the Museum of Zoology on the 19th it was almost dead.

Thrilled by this chance to handle a living Boreal Owl, I made a sketch with hard pencil on the afternoon of the 19th. The bird died during the night. I added colors to my sketch on 20 March. The drawing has been exhibited from time to time. A year or so ago I decided that the head needed flattening a little on top, for every photograph of *Aegolius funereus* that I had seen showed the bird to be somewhat flat-headed (see photo by A. Bajkov in Sutton, G. M., 1945, Condor 47: 266).

Often I have been asked about the extent to which I copy photographs when drawing birds. The statement just made answers such a question.

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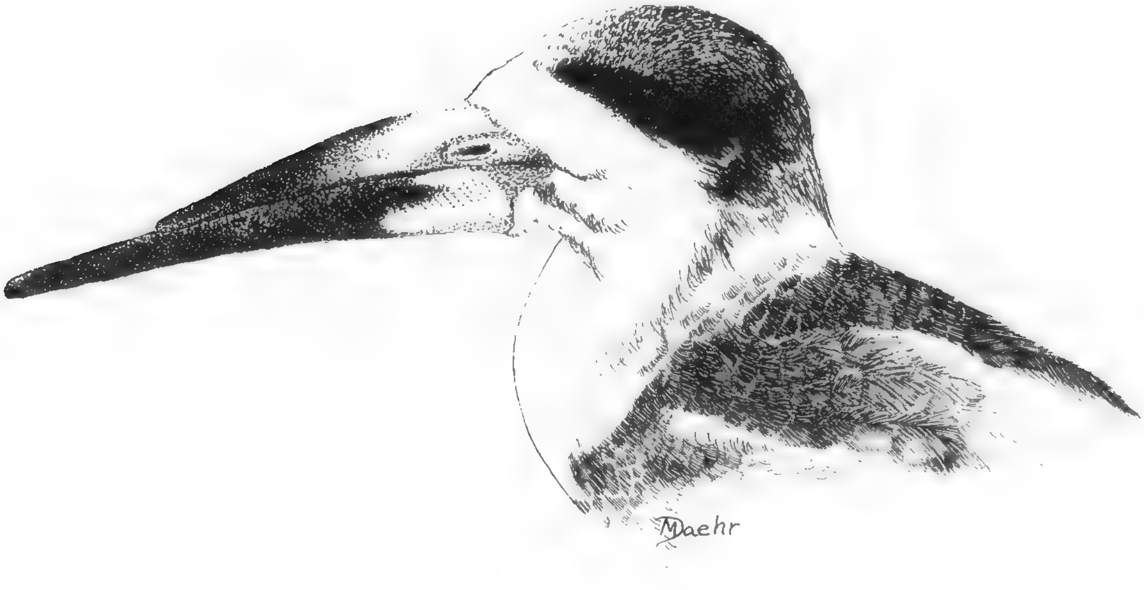


Black Skimmer, *Rynchops niger.* Drawing by David S. Maehr.

A SURVEY OF THE TYRANT FLYCATCHERS

MELVIN A. TRAYLOR, JR. AND JOHN W. FITZPATRICK

The tyrant flycatchers (Tyrannidae) form the largest and most diverse family of birds in the New World. North of Mexico the family is represented by 32 breeding species, most of which epitomize for North Americans the "true" flycatcher, a drab green or gray bird that sits quietly upright on a perch, then sallies out to catch a passing insect and returns to the same or a nearby perch to repeat the cycle. Nothing about our 32 flycatchers, however, suggests that they are indeed truly representative of the dominant and most widespread family of South American birds. Although no habitat in North America contains more than three or four species of flycatchers (e.g. Hespenheide 1971), some South American communities can contain more than 60! There are flycatchers adapted to every habitat on that continent, from sea level to snowline, and from the mountains of Venezuela south to the frigid grasslands of Tierra del Fuego. Variations run from almost aerial to fully terrestrial, and from the smallest passerine bird, the tiny warbler-like Short-tailed Pygmy-Tyrant (*Myiornis ecaudatus;* Plate 1) with an overall length of barely 75 mm (3 in.), to the Great Shrike-Tyrant (*Agriornis livida*), about 280 mm (11 in.). We hope in this paper to show the great diversity within the family and to suggest how the group could have radiated into so many ecological niches that in other continents are occupied by members of many different families.

NUMERICAL DOMINANCE OF THE FLYCATCHERS

To justify our use of the term "dominant," we must present some numbers. South America has long been known to have the richest bird fauna of any continent, with about 3,000 species recorded from the land and adjoining waters. Of this avifauna, 316 species, or about one in every ten, is a flycatcher. It is even more meaningful to examine flycatcher numbers within the Passeriformes (perching birds) as a whole because this is the order within which flycatchers most actively compete and interact. Of this group the flycatchers represent almost 18 percent, or more than one in every six species. This proportion holds from northern South America, where flycatchers number 18 and 20 percent of the perching birds in Colombia and Venezuela, respectively (Meyer de Schauensee 1950, 1951, Meyer de Schauensee et al. 1978), to the south, where the proportion is 26 percent in Argentina (Short 1975). Similarly, in Andean Peru and in lowland Brazil the flycatchers are 25 percent and 21 percent of the perching birds (Weske 1972, Pinto 1944). A still more impressive comparison is by habitat. Cocha-Cashu, in the Manu National Park, lies in undisturbed Amazonian rain forest in the lowlands of southeastern Peru. At this single site, 65 (23 percent) of the 281 species of perching birds are flycatchers (Terborgh et al. MS). At the opposite extreme of the habitat spectrum in South America, in the open temperate paramo and puna grasslands of the high Andes, almost the same proportion is found: 17 of 84 species (20 percent) are flycatchers (Vuilleumier and Simberloff 1980).

Numbers alone fail to convey a picture of how diverse in form the flycatchers are. After all, the emberizine finches form fully 16 percent of the North American perching bird fauna (Mayr and Short 1970), and this number varies as high as 18 percent in some regions (Monson and Phillips 1964, Griscom and Snyder 1955). But all the North American emberizine finches are small to medium-sized granivorous birds that differ little among themselves in form and behavior. In contrast, as shown by Keast (1972), flycatchers have radiated into niches that in other continents are occupied by birds as different as warblers, chats, bulbuls, shrikes, pipits, and broadbills, as well as other types of flycatchers (the Old World Muscicapidae). In this paper we attempt to describe the remarkable diversity of the Tyrannidae by following the framework of the most recent comprehensive classification of the family (Traylor 1977, 1979). Because 374 species are beyond our capacity to describe, or the reader's to absorb, we will treat them by mentioning the major phylogenetic groups, or "lineages," within each of the three subfamilies Elaeniinae, Fluvicolinae, and Tyranninae (Plate 2; Table 1), after first broadly discussing some of the structures and habits that occur throughout the family. Many of these we mention frequently later, while surveying the attributes of the individual flycatcher groups.

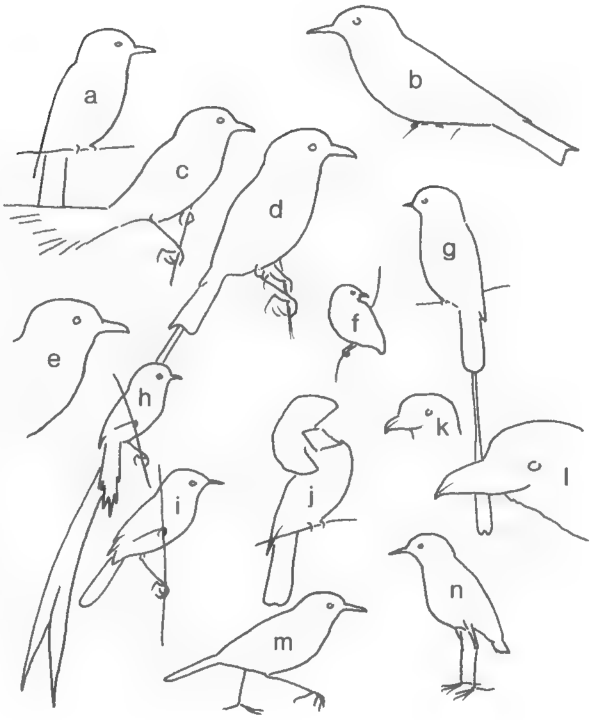
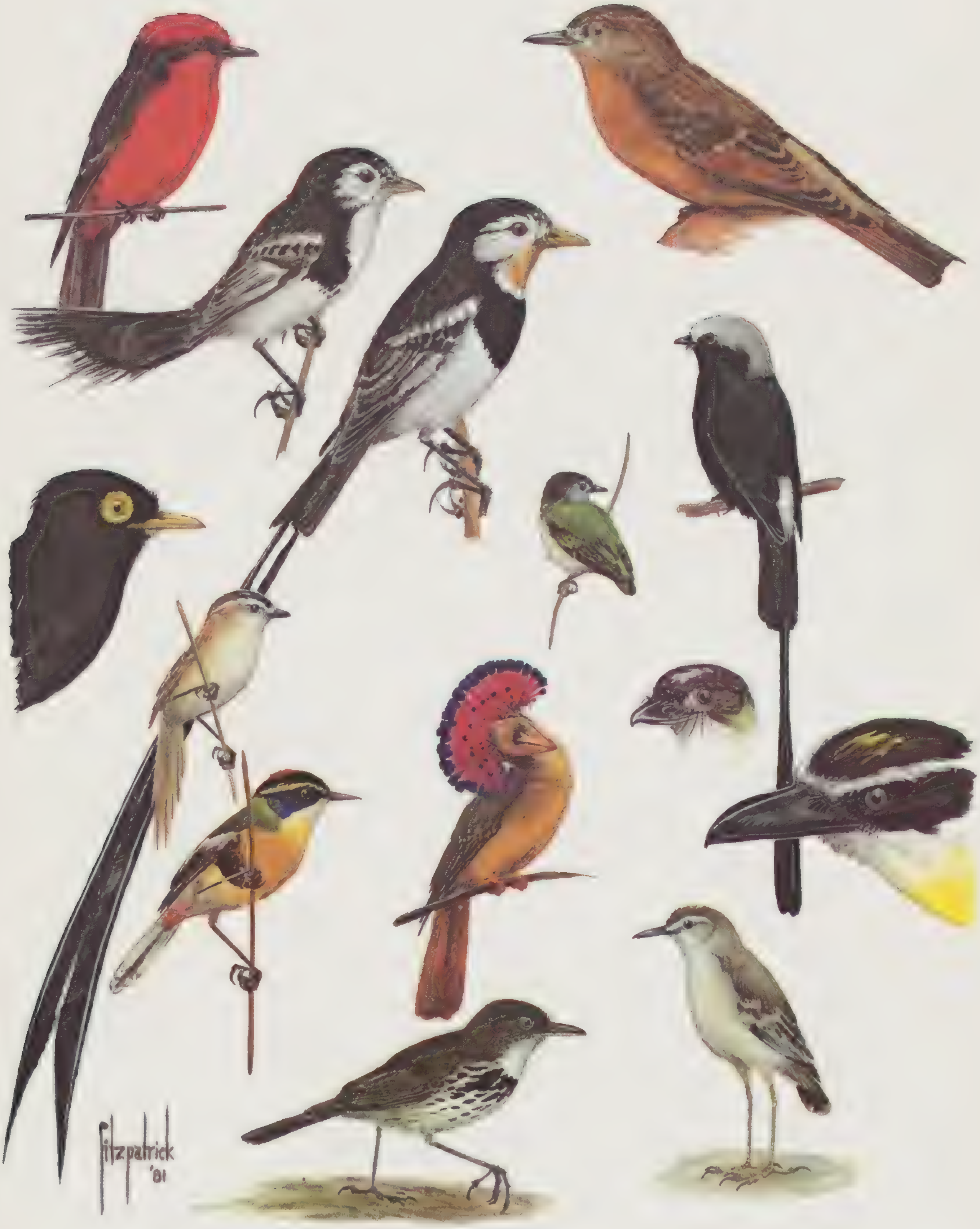


Plate 1. Not all tyrant flycatchers are medium-sized greenish birds! (a) Vermilion Flycatcher, *Pyrocephalus rubinus;* (b) Cliff Flycatcher, *Hirundinea ferruginea;* (c) Cock-tailed Tyrant, *Alectrurus tricolor;* (d) Strange-tailed Tyrant, *Alectrurus risora;* (e) Spectacled Tyrant, *Hymenops perspicillata;* (f) Short-tailed Pygmy-tyrant, *Myiornis ecaudatus;* (g) Long-tailed Tyrant, *Colonia colonus;* (h) Sharp-tailed Tyrant, *Culicivora caudacuta;* (i) Many-colored Rush-tyrant, *Tachuris rubrigastra;* (j) Royal Flycatcher, *Onychorhynchus coronatus,* in display posture; (k) White-crested Spadebill, *Platyrinchus platyrhynchos;* (l) Boat-billed Flycatcher, *Megarhynchus pitangua;* (m) Ringed Antpipit, *Corythopis torquata;* (n) Short-tailed Field-tyrant, *Muscigralla brevicauda.* Painting by John W. Fitzpatrick.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STRUCTURES AND HABITS

Foraging Modes

Ecological diversity in the flycatchers is reflected perhaps most strongly in the range of foraging styles and associated habitat preferences within the family. Flycatcher foraging behavior was comprehensively reviewed recently (Fitzpatrick 1980a, 1981a), and we will present only a brief summary here (Figure 1). Flycatchers all search for food by using some modification of a single basic procedure: they pause for varying lengths of time on a perch (or the ground), and then either move after a prey item or give up the perch to try a new one. There is no regular probing, tearing, leaf-scratching, or other active food searching; for the most part it is a passive procedure. Once spotted, prey is caught through a variety of maneuvers, and most of these rather stereotyped movements are closely associated with particular morphological adaptations.

Aerial hawking is what North Americans know as "typical" flycatcher behavior—sitting on an exposed perch, sallying out to snatch flying insects, and returning to the same spot to search again. Most flycatchers are not strictly aerial hawkers, but can be referred to as sally-gleaners. That is, they sally from a perch into the air, and then pick their prey from some substrate, not from the air itself. Thus they search their surroundings—twigs, vegetation, trunks, ground, or water—and may only rarely snatch flying prey on the wing. Among the most common forms of sally-gleaning are upward or outward hover-gleaning, and upward striking. In the former, prey is snatched from leaf surfaces during a stationary hover. In the latter, prey is literally scooped from the undersurfaces of

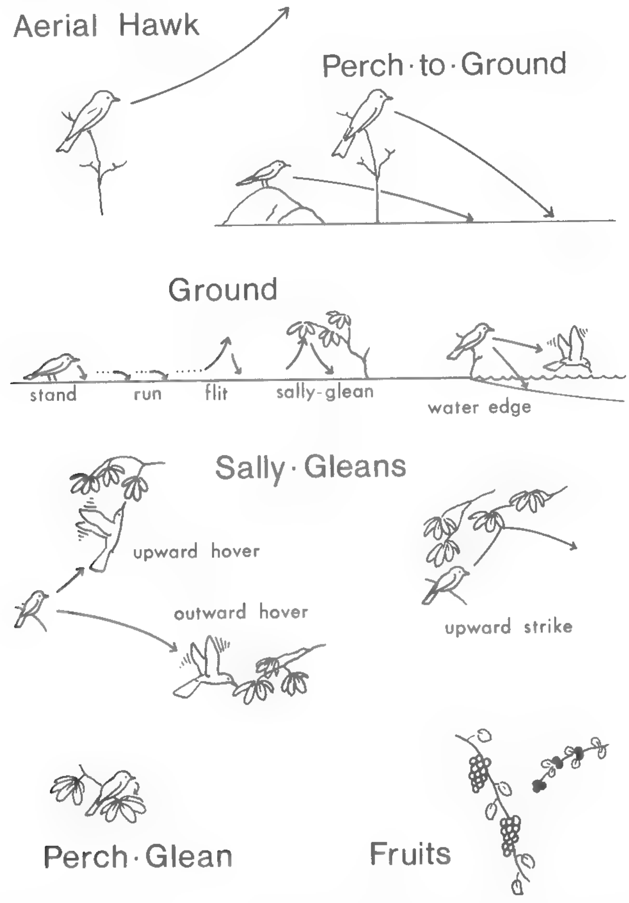


Figure 1. Prey capture techniques used by tyrant flycatchers (from Fitzpatrick 1980a, with permission). See text for explanation of terms.

leaves during a rapid flight, or strike, directly at the leaf. The other major style of gleaning foliage is referred to as perch-gleaning, which involves no sallying. Instead the prey is simply picked from some spot within the reach of the foraging bird. Many warblers and vireos also forage in this manner, and it is not surprising that flycatchers using this style extensively tend to be small, active warbler-like birds.

Many flycatchers have become partially or wholly terrestrial, and most of the prey capture techniques used by arboreal forms are also found in terrestrial ones. An intriguing example is the Ringed Antpipit, *Corythopis torquata,* which is purely terrestrial: in forests it searches not for leaf litter prey but for insects sitting on the underside of leaves above the litter, and uses the upward strike for most of its prey captures. Many open-country species have settled on a foraging style, called perch-to-ground hunting, closely resembling that of our bluebirds (*Sialia*). These species perch on elevated rocks, branches, fenceposts, wires, or rooftops and search the ground below them for insects or small vertebrates. They sally to the ground, capture their prey, and return to the elevated perch to devour it.

Fruit features heavily in the diets of only a few groups of flycatchers, but nearly all will eat some fruit occasionally. Most of the fruits that suit flycatchers are small berries plucked from vines, understory trees, and mistletoes. Figs (*Ficus* spp.) and the fruits of certain large canopy trees (e.g. in the families Anonaceae and Lauraceae) are often eaten by the larger species.

Bill Form

Because the bill of a flycatcher is its primary tool for securing food, the foraging modes just mentioned are accompanied by a corresponding variety of bill forms (Figure 2). Although there are no outlandishly bizarre bill shapes among flycatchers (except perhaps in the spadebills), each foraging mode does have a distinctive bill form that apparently is best suited to it. This has led to considerable convergence among representatives of different lineages. Convergence was not well understood by early taxonomists who, on the basis of bill shape, grouped together a number of forms now believed to be unrelated. Even our present classification may contain remnants of these errors, and the task of separating convergence from true phylogenetic affinity remains one of the problems we both are continuing to study.

The best-known flycatcher bill is the broad triangular shape characteristic of most aerial hawkers. It is found among species that hunt from exposed perches, like the kingbirds, *Tyrannus* (Figure 2a-c); in those that hawk and strike from openings within more enclosed vegetation ("enclosed perch hawkers"), such as *Empidonax* (Figure 2d); and in the highly aerial Cliff Flycatcher, *Hirundinea ferruginea* (Figure 2e; Plate 1). This bill shape is identical with that of the unrelated Old World flycatchers of the family Muscicapidae (Figure 2f) with the same aerial hawking habits.

In contrast with the broad bills of hawkers are the thin warbler-like bills of the perch-gleaners. These bills, which act more-or-less like tweezers, provide precision for picking prey items, often cryptic ones, from close range in hidden places. They are found not only in the foliage-

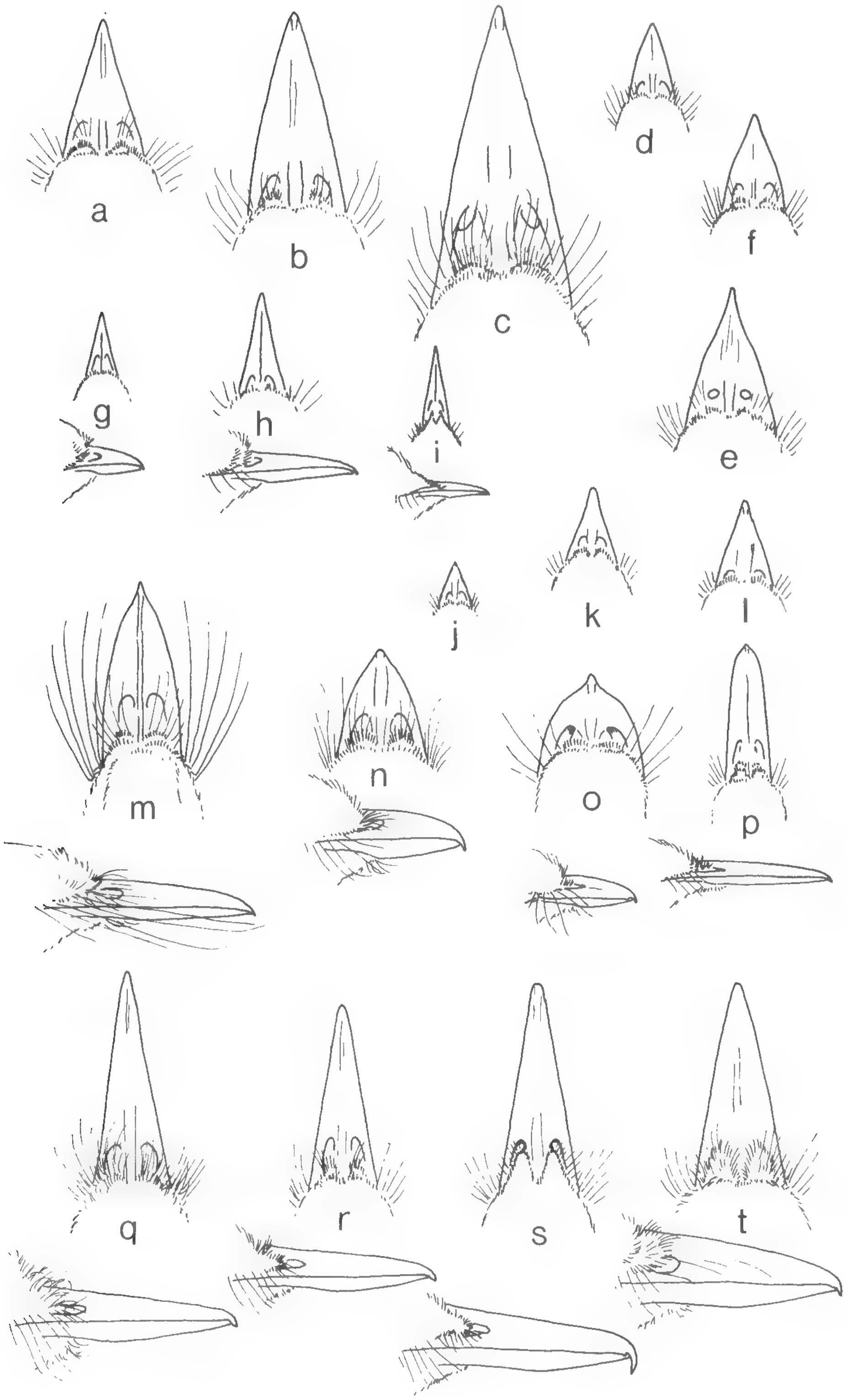


Figure 2. Some bill shapes of tyrant flycatchers. Aerial hawkers: (a) Eastern Kingbird, *Tyrannus tyrannus;* (b) Gray Kingbird, *Tyrannus dominicensis;* (c) Giant Kingbird, *Tyrannus cubensis;* (d) Least Flycatcher, *Empidonax minimus;* (e) Cliff Flycatcher, *Hirundinea ferruginea;* (f) Spotted Flycatcher, *Muscicapa striata.* Perch-gleaners and perch-to-ground salliers: (g) Northern Beardless Tyrannulet, *Camptostoma imberbe;* (h) White Monjita, *Xolmis irupero;* (i) Many-colored Rush-tyrant, *Tachuris rubrigastra.* Frugivores: (j) Golden-faced Tyrannulet, *Zimmerius viridiflavus;* (k) Yellow-bellied Elaenia, *Elaenia flavogaster;* (l) Piratic Flycatcher, *Legatus leucophaius.* Upward strikers: (m) Royal Flycatcher, *Onychorhynchus coronatus;* (n) Fulvous-breasted Flatbill, *Rhynchocyclus fulvipectus;* (o) White-crested Spadebill, *Platyrinchus platyrhynchos;* (p) Short-tailed Tody-flycatcher, *Todirostrum viridanum.* Vertebrate and large insect predators: (q) Gray-hooded Attila, *Attila rufus;* (r) Black-billed Shrike-tyrant, *Agriornis montana;* (s) Gray-bellied Shrike-tyrant, *Agriornis microptera.* General, corvid-like predator: (t) Great Kiskadee, *Pitangus sulphuratus.*

gleaning species like the beardless tyrannulets, *Camptostoma* (Figure 2g), but also in the perch-to-ground feeders like the monjitas (*Xolmis;* Figure 2h), which need the same precision for picking prey off the ground after sallying, and in the palustrine, warbler-like rush-tyrant, *Tachuris* (Figure 2i).

Flycatchers that regularly eat fruit, including some species that are truly frugivorous over much of the year, tend to have short, somewhat broadened bills (Figure 2j-1). In this way they resemble the manakins (Pipridae), which are virtually exclusively frugivorous. Examples include the Piratic Flycatcher, *Legatus leucophaius,* as well as species in the genera *Elaenia, Mionectes,* and *Muscipipra.*

Upward striking is associated with the most peculiar tyrannid bill shapes. These bills all are extremely broad, but their length may vary from three times the width, as in some tody-flycatchers (*Todirostrum;* Figure 2p), to barely half the width, as in spadebills (*Platyrinchus;* Figure 2o). The bill may be spatula-shaped with parallel edges (*Todirostrum*) or a broad triangle with swollen mandible (e.g. *Rhynchocyclus;* Figure 2n). These spoon-like bills allow the bird to scoop prey from the undersides of leaves during an explosively rapid upward strike. Rictal bristles are also pronounced among these species, which suggests that they too are tied somehow to the upward striking habit. The extreme form of both bill and bristle development is found in the Royal Flycatcher (*Onychorhynchus;* Figure 2m).

Some flycatchers take a generalized diet that includes large insects, including moths and katydids, and even lizards and frogs. These species have relatively long, strong bills whether they live in forests (e.g. *Attila;* Figure 2q) or open temperate grasslands (e.g. the shrike-tyrants, *Agriornis;* Figure 2r). The latter genus also contains some very large species with shrike-like foraging styles and, as do the shrikes, they possess a powerful bill equipped with a large hook at the tip (Figure 2s).

It has been said that "jacks-of-all-trades are masters of none." This maxim applies well to the shape of flycatcher bills. A number of species use a variety of prey capture techniques without specializing on any one. These flycatchers, regardless of their relationships to other more specialized forms, show perfectly "average" bill shapes in every dimension, e.g. the Great Kiskadee, *Pitangus sulphuratus,* Figure 2t (Fitzpatrick 1978).

Voice and Display

Flycatchers are notably undistinguished songsters. They share with the other "non-oscine" passerines a relatively simple syrinx in contrast with the more elaborate vocal apparatus of the true songbirds, the "oscines." Perhaps as a result (although this is not well established), the non-oscines generally utter simple phrases that often sound unmusical. Flycatcher songs mostly consist of one or a few weakly whistled or warbled notes. Sometimes these are arranged into phrases or trills, but rarely have a complicated pattern and almost never would be described as beautiful. In general the songs are higher-pitched and slightly more varied than the monotonous series of ascending or descending whistles and clucks typical of some of the other non-oscines, the ovenbirds and antbirds (Furnariidae and Formicariidae). As shown by Stein (1958), however, even the simple songs of flycatchers can be crucial species-specific isolating mechanisms between very similar and closely related forms.

Vocal qualities vary considerably among flycatcher groups. Mechanical, sometimes metallic, "tick" sounds characterize the tody-tyrants. Insignificant twittering "peep"s and trills are offered by many genera in the Elaeniinae (e.g. *Phyllomyias, Phylloscartes,* and relatives) and Fluvicolinae (e.g. *Ochthoeca, Empidonax, Pyrrhomyias*). Soft whistles characterize most flatbills. The familiar "pee-o-weeee" song of the Eastern Wood Pewee typifies vocal qualities in that genus (*Contopus*). Some spadebills (*Platyrinchus*) and pygmy-tyrants (*Myiornis*) have such high-pitched weak trills that they cannot easily be separated from insect sounds in the tropical forest. Whistles become shrill or warbled in *Elaenia* and *Myiarchus.* The most raucous calls belong to the Great Kiskadee and its relatives. The shouted "Kis-ka-dee!" has been translated by other cultures into *"Christo-rey"* (Christ the King), *"Christo-fué"* (Christ has gone), and *"Bém-ti-vi"* (saw you well; part of a Brazilian legend about the watchful kiskadee befouling a runaway thief).

One particular vocal feature—the dawn song—sets the Tyrannidae apart from most other tropical birds. This phenomenon can be heard early in the morning even among temperate North American pewees, crested flycatchers, and kingbirds, but comes into its own in the tropics. In the very first light of a South American dawn, flycatchers are among the first birds to begin singing. Almost all species, from the smallest tyrannulets to the largest kingbirds and relatives, utter distinct dawn songs in a fashion not repeated at other times of the day. Frequently these songs resemble more typical daytime songs, but equally often are unique in the species' repertoire, uttered only during a ten-minute "waking-up" period as the sky first lightens. Usually these dawn songs are short loud phrases repeated over and over while the bird remains on a single perch. Dawn songs are so stereotyped and species-specific that a recent major taxonomic revision of the genus *Myiarchus* included a key to the species based solely on the acoustical features of their respective dawn songs (Lanyon 1978: 448).

All flycatchers produce simple vocalizations in addition to their primary song. Most typically these are simple "chip" or "peep" notes uttered as contact notes between members of a pair. Vocalizations are also given in many other contexts, thus flycatcher vocal repertoires have been the subject of some important theoretical work in animal communication, notably that of W. J. Smith (1969, 1970b, 1970c).

A few species sing peculiar songs in conjunction with courtship or territorial displays. A well-studied example is that of the Vermilion Flycatcher (*Pyrocephalus rubinus;* Plate 1), in which the male launches into long aerial flights over open fields during the breeding season. In flight the wings are often held up over the back, providing a fluttery, butterflylike appearance while the bird sings a long jumbled series of sweet whistles and warbles (Smith 1967, 1970a). The Streamer-tailed Tyrant (*Gubernetes yetapa*) utters piercing whistles, warbles, and bill-popping sounds in a mutual display between male and female while both sexes bob up and down on a perch, flap their wings, and alternately raise and lower their long tails. Wing-flapping is a common element in displays throughout the family, often in conjunction with vociferous calling and crest displaying. Some species exaggerate certain portions of this wing-flapping by holding the wings outstretched or flapping them broadly and stiffly while perched and calling (e.g. *Fluvicola, Ochthoeca*). Others flutter them rapidly either in flight (e.g. *Tyrannus;* Smith 1966) or on a perch (e.g. *Pitangus*). Tody-tyrants have a speeded-up version of wing-flapping that actually can produce a buzzing sound.

The strangest, most elaborate displays in the family are those of certain fluvicoline species that inhabit open marsh or scrub areas of southern Brazil, northern Argentina, and the Paraguayan chaco. These displays are exemplified by the Spectacled Tyrant (*Hymenops perspicillata;* Plate 1). As described by Hudson (1920: 160) these black birds "perch on a conspicuous place, upright, motionless, and looking more like grotesque little automata than living things; as if shot from [the perch] by means of a steel spring ... it darts vertically to a height of about fifteen yards, then turns a somersault, uttering at the same moment a shrill little cry, after which it drops down again and alights on its perch suddenly, as if jerked back to it ..." Similar displays are known in the black tyrants (*Knipolegus*), and slight variations characterize the genera *Alectrurus* and *Arundinicola* (Fitzpatrick unpubl. obs.).

Nest Forms

Recognition of the importance of nest form as an indicator of relationships within the flycatchers dates to 1904, when Ihering divided a previously recognized subfamily into two new ones on the basis of their different nest structures, either cup-shaped or pendant. It is remarkable how well Ihering's subfamilies still stand together as clearly related lineages—the "*Serpophaga,*" and the "tody-tyrant" and "flatbill" groups, respectively—even within the present, completely revised classification. It is apparent that nest form remained one of the more conservative features of flycatcher biology during their explosive ecological and morphological radiation. This is also believed to be true of other non-oscines, like the ovenbirds (Furnariidae; Vaurie 1980).

The most common, probably primitive, nest type is the open cup (Figure 3a-e), appearing in a bewildering diversity of forms and locations, all based on the same general structure. Cup nests may be high and conspicuous in trees (as in those of many kingbirds), or low and well concealed in foliage. Some are loose and untidy (e.g. Alder Flycatcher, *Empidonax alnorum;* Figure 3a); others are carefully woven, tight, beautiful little cups as in those of the pewees, *Contopus* (Figure 3b), and in the genus *Elaenia.* They may be placed on the ground among rocks (e.g. the ground-tyrants, *Muscisaxicola),* or among clumps of grass (*Neoxolmis;* Figure 3c). Several species, including our phoebes (Figure 3d) place them in sheltered niches on cliff faces. The Spectacled Tyrant (*Hymenops*) builds a cup in reeds over water. The most elegant cup nest is that of the Many-colored Rush-tyrant (*Tachuris rubrigastra;* Figure 3e); it is a delicate cone-shaped structure attached along one side to a single reed.

The covered, ball-shaped nest with a side entrance apparently has evolved independently in all three subfamilies. Among the Elaeniinae, the Beardless Flycatcher (*Camptostoma*) builds a small ovoid nest concealed in low vegetation; in the Fluvicolinae, *Fluvicola* (Figure 3f) and *Arundinicola* build loose globular nests of grass placed over water; and in the Tyranninae, *Pitangus sulphuratus* (Figure 3g) places its bulky, ball-shaped nest conspicuously in low trees. Its close relative the Lesser Kiskadee, *P. lictor,* is

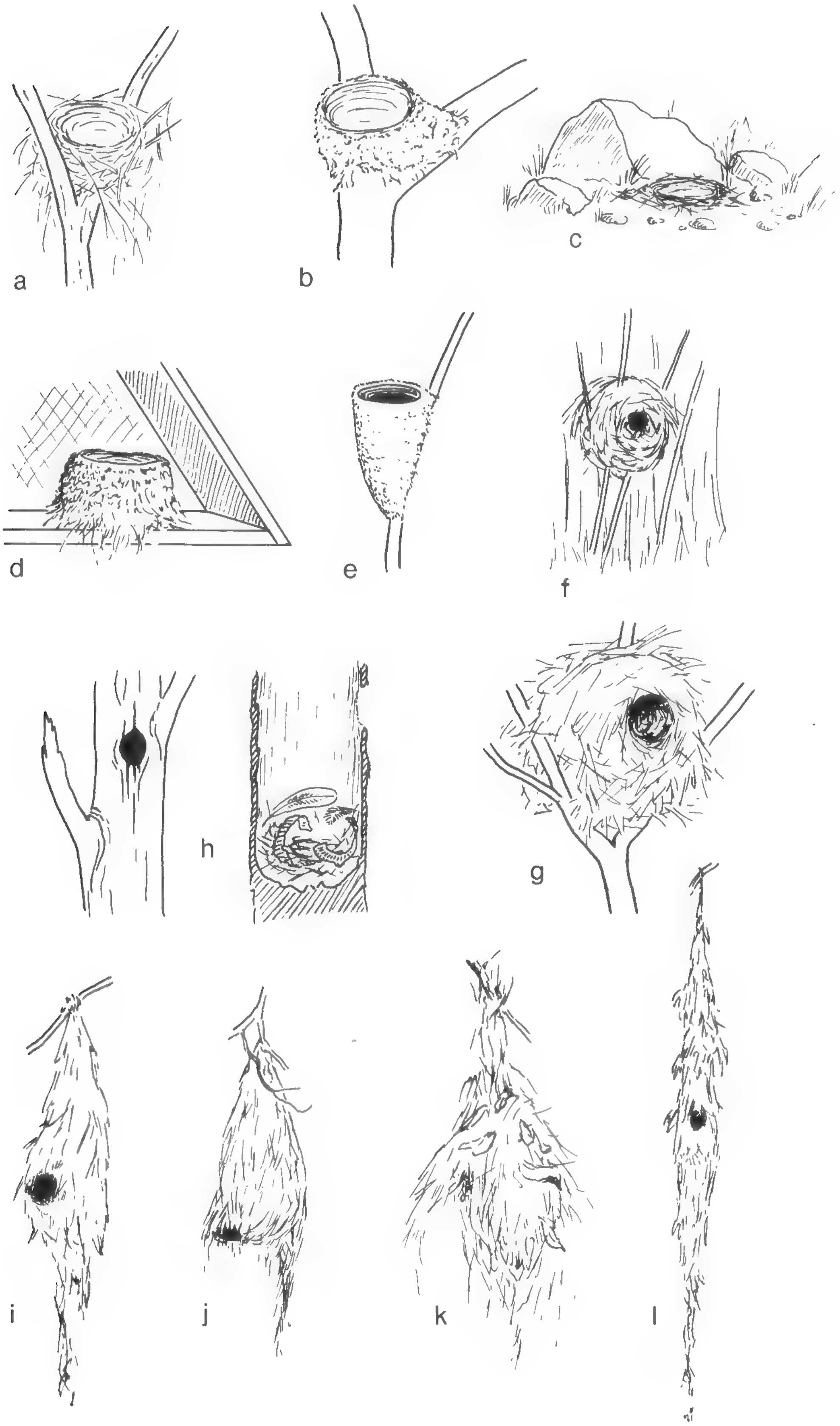


Figure 3. Types of nests built by tyrant flycatchers. Cup-shaped: (a) Alder Flycatcher, *Empidonax alnorum;* (b) Eastern Wood Pewee, *Contopus virens;* (c) Chocolate-vented Tyrant, *Neoxolmis rufiventris;* (d) Eastern Phoebe, *Sayornis phoebe;* (e) Many-colored Rush-tyrant, *Tachuris rubrigastra.* Covered: (f) Pied Water-tyrant, *Fluvicola pica;* (g) Great Kiskadee, *Pitangus sulphuratus.* In holes: (h) Great Crested Flycatcher, *Myiarchus crinitus,* showing outside and section through cavity. Pendant: (i) Pearly-vented Tody-tyrant, *Hemitriccus margaritaceiventer;* (j) Yellow-olive Flycatcher, *Tolmomyias sulphurescens;* (k) Black-tailed Flycatcher, *Myiobius atricaudus;* (l) Royal Flycatcher, *Onychorhynchus coronatus.*

known to build a more typical cup nest, but occasionally constructs one with a partial dome (Smith 1962). Furthermore, *P. sulphuratus* has been seen building a perfectly normal open cup, which it then gradually covered over during the first two weeks of incubation (Fitzpatrick unpubl. obs.). Therefore, the distinction between cup and ball nests appears not to be especially rigid, and the evolutionary pathway from one to the other is clear.

Hole-nesting occurs in several genera, all except the Long-tailed Tyrant (*Colonia*) being in one subfamily (Tyranninae). The White-ringed Flycatcher (*Conopias parva*), besides using holes, sometimes uses abandoned cacique (Icteridae) nests. The related Piratic Flycatcher (*Legatus*) usurps active, covered ones for its own use. The Sulphur-bellied Flycatcher and its relatives (*Myiodynastes*) always nest in holes, and the related Social Flycatcher (*Myiozetetes similis*) occasionally places its bulky grass nest (usually round and exposed) inside large holes, which is again suggestive of an evolutionary pathway toward hole-nesting. The genus *Myiarchus* (Figure 3h), including our Great Crested and Ash-throated flycatchers, is the best known group of hole-nesters. All share the peculiar habit of adding a bit of reptile skin, and usually some animal hair or feathers, to the nest lining. The Galapagos form, *M. magnirostris,* suffers a shortage of holes because no woodpeckers occur on those islands. It may use the abandoned domed nests of Darwin's Finches, and adds hair and feathers. This tame species has been photographed trying to make off with some human hair, still attached (Lanyon 1978)!

The most elaborate and derived nests are the pendant, pyriform nests suspended from an overhanging twig by plant fibers (Figure 3i-l). These are purse-shaped nests with a side entrance, and they often have a long tail of loose fibers dangling below. Considerable intergeneric variation occurs in these nests, usually in the form and placement of the entrance. These nests are often well camouflaged amongst debris, twigs, or root banks, but that of the Common Tody-flycatcher, *Todirostrum cinereum,* is hung high in shrubs or trees, with little attempt at concealment. The pendant form is the only one known among the tody-tyrants (Figure 3i) and, except for *Platyrinchus,* the related flatbills (Figure 3j). The pendant nest is also built by several fluvicoline genera (e.g. *Myiobius,* Figure 3k, and *Onychorhynchus,* Figure 3l), apparently through independent evolution.

Wing Feather Modifications

One characteristic of particular interest in the flycatchers is the recurring tendency to develop peculiarly shaped wing feathers. Apparently the genetic control of the form of the primaries is extremely plastic, for oddly shaped feathers occur in all the major flycatcher lineages almost at random. The affected feathers may be narrow and blade-shaped, narrow and pointed, only half normal length, slightly to deeply notched at the tip, notched subterminally on the inner webs, truncated at the tip, or twisted. Although typically only the outer primaries are affected, some species have normal outer feathers but several abnormal inner ones. Intrageneric variation is great, both in presence or absence of modifications, and in their exact form. In the Fork-tailed Flycatcher, *Tyrannus savana,* all four subspecies have a different notching pattern. In most taxa these peculiar feathers are confined to males, although in a few they are found, or more

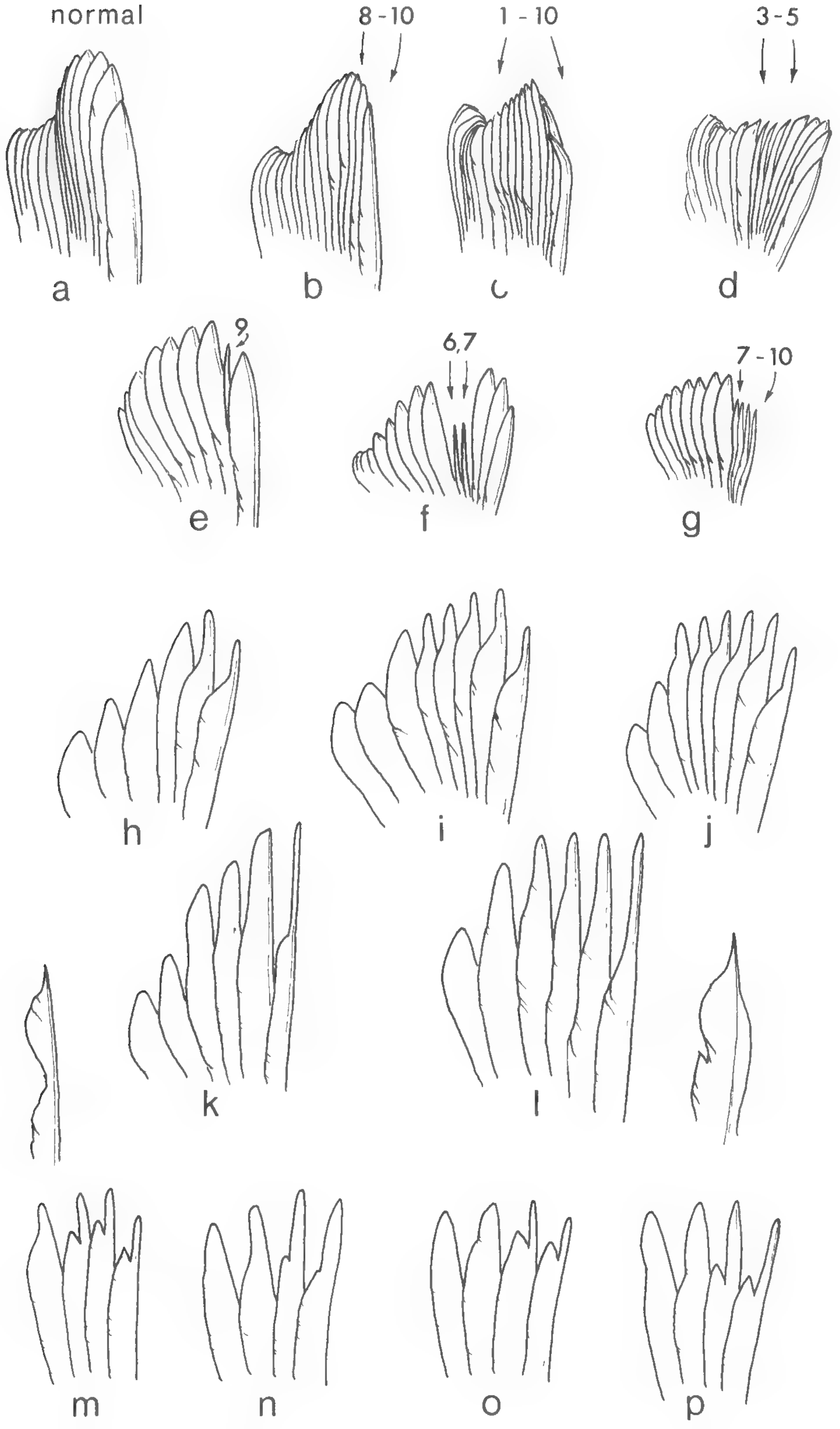


Figure 4. Some aberrant wing feathers found among the tyrant flycatchers. The primaries are numbered one to ten from the inside out. (a) Blue-billed Black-tyrant, *Knipolegus cyanirostris;* (b) Hudson's Black-tyrant, *K. hudsoni;* (c) Cinereous Tyrant, *K. striaticeps;* (d) Subtropical Doradito, *Pseudocolopteryx acutipennis;* (e) Streak-necked Flycatcher, *Mionectes striaticollis;* (f) Crested Doradito, *Pseudocolopteryx sclateri;* (g) Pale-eyed Pygmy-tyrant, *Atalotriccus pilaris;* (h) Eastern Kingbird, *Tyrannus tyrannus;* (i) White-throated Kingbird, *T. albogularis;* (j) Gray Kingbird, *T. dominicensis;* (k) Scissor-tailed Flycatcher, *T. forficata;* (l) Western Kingbird, *T. verticalis;* (m) Fork-tailed Flycatcher, *T. savana savana;* (n) *T. s. sanctaemartae;* (o) *T. s. monachus;* (p) *T. s. circumdatus;* (m) through (p) are from Zimmer (1937). Individual feathers: (left) Cock-tailed Tyrant, *Alectrurus tricolor,* ninth primary; (right) Black-and-white Monjita, *Xolmis dominicana,* tenth primary.

often merely suggested, in the females; in no species do aberrant primaries occur only in females.

Figure 4 illustrates some of the peculiarities just mentioned. In *Knipolegus* (Figure 4a-c) most species have normal wings, but male *hudsoni* and *poecilocercus* have three narrowed outer primaries and *striaticeps* has all ten modified. Modified inner primaries, with normal outer ones, are shown by some of the "doraditos" (*Pseudocolopteryx;* Figure 4d) and the genus *Mionectes* (Figure 4e). The most extreme feather reduction occurs in the Pale-eyed Pygmy-tyrant (*Atalotriccus pilaris;* Figure 4g), whose four outer primaries are so greatly reduced that they barely resemble flight feathers at all. The Crested Doradito (*Pseudocolopteryx sclateri;* Figure 4f) has two similarly reduced inner primaries. The two single feathers shown in Figure 4, the ninth primary of *Alectrurus tricolor* (left) and the tenth primary of *Xolmis dominicana* (right), fit no particular pattern.

The kingbirds (*Tyrannus;* Figure 4h-p) illustrate variation in notching of the primary tips, which may have evolved from normal "slotting" of wing tips for aerodynamic reasons. They also show that closely related forms may have quite different patterns. Among the 13 species, the outer two, five, or six primaries may be notched (Figure 4h-j), but both sexes of one species, the Loggerhead Kingbird (*T. caudifasciatus*), have completely normal primaries. Other variations also occur in this single genus. Examples include the attenuated outer primaries of the Scissor-tailed Flycatcher and Western Kingbird, *Tyrannus forficata* (Figure 4k) and *verticalis* (Figure 4l), and the four different subspecies of the Fork-tailed Flycatcher, *T. savana* (Figure 4m-p).

Although in the past these abnormal feathers were used by taxonomists as generic characters, it is obvious from the patterns in *Tyrannus* and other groups that, at best, they are reliable only as specific or subspecific characters. The function of these abnormal feathers is difficult to understand. Since they often occur only in males, they probably are associated primarily with wing displays because throughout the family, rapid wing fluttering has been recorded as a conspicuous feature of courtship and territorial displays. For example, the wings of the pygmy-tyrant *Atalotriccus pilaris,* frequently produce a whirring buzzy sound, presumably aided by the strange outer primaries. In many cases, however, closely related species with similar display patterns vary widely in the degree to which the primaries are modified. Clearly, there is much still to be learned about the biological significance of these structures.

A SURVEY OF THE TYRANNIDAE

Our most recent classification recognizes 87 genera and 374 species of tyrant flycatchers (Traylor 1979), which are divided into three subfamilies—Elaeniinae, Fluvicolinae, and Tyranninae (Table 1). (An interesting taxonomic problem still remains with the two genera of tityras and becards that compose the Tityrinae, included with the flycatchers in Peters' Check-list; *Tityra* and *Pachyramphus* are only distantly related to the rest of the family, and traditionally have been placed with the Cotingidae. They will not be considered here.) Plate 2 shows typical representatives of the major lineages of the Tyrannidae, occupying their respective positions in the phylogenetic tree.

We of course have no direct evidence of what the primitive proto-flycatchers looked like or how they acted. However, based on the appearance and behavior of the presumed primitive flycatcher relatives in the manakins and cotingas (Pipridae and Cotingidae), the earliest flycatcher probably was a small, greenish, primarily insectivorous forest bird; it most likely fed by gleaning insects from small twigs and leaves and sometimes by darting after flying insects. The primitive flycatchers probably also frequented understory fruiting trees and vines to eat berries, much as most manakins and many flycatchers do today. This description of a hypothetical tyrannid ancestor actually fits many modern-day representatives of the subfamily Elaeniinae. We begin our survey with this apparently primitive subfamily. Table 1 provides a summary of the current classification of flycatchers, including information on relationships within subfamilies, and generic distribution of habitat preferences, nest forms, foraging modes, and general distribution patterns.

The previous "standard" classification of the flycatchers, that of Berlepsch (1907) and Hellmayr (1927), was based primarily on external morphology and on nest form, the latter following Ihering (1904). The current classification (Traylor 1977) was built on the foundation of Berlepsch and Hellmayr, but also relied heavily on Warter's (1965) studies of cranial characteristics and Ames' (1971) report on syringeal anatomy (Table 2). As the table shows, syringeal and cranial structures show reasonably close agreement in defining groups of related species, even within the subfamilies. Broad categories of foraging behavior also conform well to these groupings (Fitzpatrick 1980a).

Table 2 shows that it is still impossible to provide a technical diagnosis for all the subfamilies, although the Tyranninae can be defined as having the unique combination of Warter's type 1 or 2 nasal septum and type 1 interorbital septum and palatine. The fluvicolines are primarily defined by the type 6 nasal septum which is found in all but three genera and also in a few Elaeniinae. The latter group is partially described by the type 4 interorbital septum—all that possess it are Elaeniinae, but it occurs in only a few of the *Elaenia* group itself. Fortunately, our confidence in the current classification is reinforced by the close correlation between the lineages determined from Hellmayr's and Warter's classifications and Ames' groups of genera, but we realize that the ultimate classification has not yet been achieved.

Elaeniinae

Although the Elaeniinae contains almost half the species of flycatchers (180), it is the least represented in North America. Only the Beardless Flycatcher, *Camptostoma imberbe,* reaches our area, and only along the Mexican border.

The Elaeniinae has less morphological or behavioral variation than do either of the other subfamilies. Species vary from the "microscopic" to the medium-sized. The majority varies only minimally from the "little green flycatcher" plumage pattern: dark olive above, paler olive to yellowish below, with variable facial markings, wing bars, and crown colors. Thus a bewildering array of look-alikes is included in this lineage, most of which are known as tyrannulets (Meyer de Schauensee 1966). We recommend that the interested reader study Plates 29 and 30 in Meyer de

TABLE 1

The Genera of Tyrant Flycatchers, with Notes on Habitat, Nest Form, Foraging Behavior, and Distribution

Taxa	*No. species*	*Habitats*[1]	*Nest form*[2]	*Foraging mode*	*Distribution*[3]
Subfamily **ELAENIINAE**					
"*Elaenia*" group					
Phyllomyias	10	woodland, forest (t,s)	2; open cup	fruit; up hover-glean	C.A., Andes, Amazonia
Zimmerius	5	forest (t,s)	2; ovoid, pensile	fruit; up hover-glean	C.A., Andes, Amazonia
Ornithion	3	forest (t)	1; shallow cup	perch-glean	C.A., northern S.A.
Camptostoma	2	scrub, forest edge (t)	2; globular	perch-glean	N.A. to southern S.A.
Phaeomyias	1	scrub, forest edge (t)	1; open cup	fruit; up hover-glean	C.A. to southern S.A.
Sublegatus	2	scrub, forest edge (t)	2; shallow cup	outward hover-glean	C.A. to southern S.A.
Suiriri	1	woodland, cerrado (t)	1; shallow cup	perch-glean	southern S.A.
Tyrannulus	1	forest canopy (t)	1; shallow cup	fruit; up hover-glean	C.A., northern S.A.
Myiopagis	7	forest, woodland (t)	4; open cup	fruit; perch-, hover-glean	W.I., C.A. to southern S.A.
Elaenia	17	forest to scrub (t,s)	13; neat cup	fruit; perch-, hover-glean	W.I., C.A. throughout S.A.
"*Serpophaga*" group					
Mecocerculus	6	montane forest (s)	unknown	perch-, hover-glean	Andes, tepuis
Serpophaga	5	woodland; stream bank (t,s)	3; open cup	perch-glean	C.A., Andes, to so. S.A.
Inezia	3	scrub, mangrove, edge (t)	1; open cup	perch-glean	no. and so. S.A.
Stigmatura	2	brush, forest edge (t)	1; shallow cup	perch-glean	Amazonia, so. S.A.
Anairetes	7	temperate scrub (s,p)	3; open cup	perch-, hover-glean	Andes, Patagonia
Tachuris	1	reedy marshes (t,p)	1; neat cone	perch-glean	arid coast, Andes, so. S.A.
Culicivora	1	grasslands (t)	1; open cup	generalist	southern S.A.
Polystictus	2	grasslands (t)	1; open cup	unknown	no. and so. S.A.
Pseudocolopteryx	4	marshes (t)	3; deep cup	perch-glean	so. S.A., Andes
Euscarthmus	2	arid scrub (t)	1; shallow cup	perch-glean, strike	no., so. S.A., arid coast
"Transitional" groups					
Mionectes	5	forest, woodland (t,s)	4; pensile purse	fruit; up hover-glean	C.A., throughout S.A.
Leptopogon	4	forest, woodland (t,s)	2; pensile globe	fruit; up hover-glean	C.A., throughout S.A.
Phylloscartes	19	forest (s,t)	1; part-domed cup	up hover-glean, strike	C.A., Andes, se. Brazil

TABLE 1 (continued)

The Genera of Tyrant Flycatchers, with Notes on Habitat, Nest Form, Foraging Behavior, and Distribution

Taxa	*No. species*	*Habitats*[1]	*Nest form*[2]	*Foraging mode*	*Distribution*[3]
"Transitional" groups (continued)					
Pseudotriccus	3	forest undergrowth (s)	unknown	up strike	Andes
Corythopis	2	forest, terrestrial (t)	1; oven-shaped	up strike	Amazonia, se. Brazil
"Tody-tyrant" group					
Myiornis	3	forest (t)	2; pensile purse	up strike, hover-glean	C.A., Amazonia, so. S.A.
Lophotriccus	4	forest (t,s)	3; pensile purse	up strike	C.A., Andes, Amazonia
Atalotriccus	1	scrub, woodland (t)	1; pensile purse	up strike	C.A., no. S.A.
Poecilotriccus	4	forest, bamboo (s,t)	unknown	up strike	Andes, Amazonia
Oncostoma	2	scrub, woodland (t)	1; pensile purse	up strike	C.A.
Hemitriccus	19	forest, woodland, scrub (t,s)	3; pensile purse	up strike	Andes, no. through so. S.A.
Todirostrum	14	edge, scrub, mangrove (t)	7; pensile purse	up strike	C.A. to so. S.A.
"Flatbill" group					
Cnipodectes	1	forest (t)	1; pensile	unknown	C.A., Amazonia
Ramphotrigon	3	forest, bamboo (t)	unknown	up strike	Amazonia, so. S.A.
Rhynchocyclus	3	forest (t,s)	2; pensile purse	up strike	C.A. to so. S.A.
Tolmomyias	4	forest, woodland (t)	3; pensile purse	up strike	C.A. to so. S.A.
Platyrinchus	7	forest, woodland (t,s)	2; neat cup	up strike	C.A. to so. S.A.
Subfamily **FLUVICOLINAE**					
"*Myiobius*" group					
Onychorhynchus	1	forest, woodland (t)	1; long, pensile	up strike	C.A., no. through so. S.A.
Myiotriccus	1	forest (s)	unknown	encl. perch hawk	Andes
Terenotriccus	1	forest (t)	1; pensile	up strike	C.A. through Amazonia
Myiobius	3	forest (t,s)	2; pensile purse	"redstart" style, hawk	C.A. through so. S.A.

TABLE 1 (continued)

The Genera of Tyrant Flycatchers, with Notes on Habitat, Nest Form, Foraging Behavior, and Distribution

Taxa	*No. species*	*Habitats*[1]	*Nest form*[2]	*Foraging mode*	*Distribution*[3]
Subfamily **FLUVICOLINAE** (continued)					
"*Empidonax*" group					
Myiophobus	9	forest, woodland (s,t)	1; open cup	encl. perch hawk	Andes, C.A. through so. S.A.
Aphanotriccus	2	forest (t)	unknown	encl. perch hawk	C.A.
Xenotriccus	2	woodland (s)	2; open cup	unknown	C.A.
Hirundinea	1	mountain cliffs (s)	1; cup on ledge	aerial hawk	Andes, tepuis, so. S.A.
Pyrrhomyias	1	forest openings (s)	1; cup in niche	aerial hawk	Andes
Mitrephanes	2	forest openings (s)	1; shallow cup	aerial hawk	C.A., Andes
Contopus	10	forest, woodland (t,s)	7; neat shallow cup	aerial hawk	N.A. through so. S.A., W.I.
Empidonax	16	woodland, scrub	14; open cup	encl. perch hawk	N.A. through so. S.A.
Nesotriccus	1	woodland (t)	1; open cup	unknown	Cocos Island
Cnemotriccus	1	woodland, scrub (t)	1; cup	encl. perch hawk	no. through so. S.A.
"Transitional" group					
Sayornis	3	woodland, streams	3; sheltered cup	near-ground generalist	N.A. through Andes
Pyrocephalus	1	open country, edges (t)	1; shallow cup	near-ground generalist	N.A. through so. S.A.
"Ground-tyrant" group					
Ochthoeca	11	forest, temperate scrub (s,p)	4; cup or pensile	near-ground generalist	Andes, Amazonia
Myiotheretes	6	cloud forest (s)	unknown	near-ground generalist	Andes
Xolmis	6	open woodland, cerrado (t)	4; cup	perch-to-ground	so. S.A. to Patagonia
Neoxolmis	2	temperate grassland (p)	1; cup on ground	perch-to-ground	Patagonia
Agriornis	5	temperate grassland (p)	3; bulky cup in rocks	perch-to-ground	Andes, Patagonia
Muscisaxicola	12	high Andean puna (p)	10; cup in niche	ground picking, sallying	Andes, Patagonia, Amazonia
Muscigralla	1	arid littoral	1; domed on ground	ground picking, sallying	arid coastal Peru

TABLE 1 (continued)

The Genera of Tyrant Flycatchers, with Notes on Habitat, Nest Form, Foraging Behavior, and Distribution

Taxa	*No. species*	*Habitats*[1]	*Nest form*[2]	*Foraging mode*	*Distribution*[3]
"*Fluvicola*" group					
Lessonia	2	temperate moist grass (t,p)	2; cup on ground	ground picking, sallying	Andes, Patagonia
Knipolegus	10	woodland, forest (s,t)	3; cup	near-ground, aerial hawk	Andes, no. through so. S.A.
Hymenops	1	open marshland (t)	1; cup in reeds	ground, perch-to-ground	so. S.A.
Fluvicola[4]	2	marsh (t)	2; ball over water	near-ground generalist	no. through so. S.A.
Arundinicola[4]	1	marsh (t)	1; ball over water	aerial hawk, water-snatch	no., so. S.A.
Colonia	1	woodland, edge (t)	1; hole in tree	aerial hawk	C.A. through so. S.A.
Alectrurus	2	grassland (t)	2; cup on ground	aerial hawk, strike	so. S.A.
Gubernetes	1	grassland, edge (t)	1; cup on ground	aerial hawk	so. S.A.
Uncertain affinities					
Satrapa	1	open woodland (t)	1; cup	fruit; aerial hawk?	so. S.A.
Tumbezia	1	arid scrub (t)	unknown	near-ground generalist?	arid coastal Peru
Machetornis	1	open grassland (t)	1; holes or old nests	ground, follows livestock	no., so. S.A.
Muscipipra	1	forest, woodland (s, t)	unknown	fruit; aerial hawk	southeastern Brazil
Subfamily **TYRANNINAE**					
"*Myiarchus*" group					
Attila	7	forest, woodland (t)	3; cup in tree cleft	outward hover-glean	C.A. through so. S.A.
Casiornis	2	woodland, scrub (t)	1; hole in tree	outward hover-glean	southern S.A.
Rhytipterna	3	forest (t)	unknown	outward hover-glean	C.A. through Amazonia
Laniocera	2	forest (t)	unknown	fruit; hover-glean	C.A. through Amazonia
Sirystes	1	forest canopy (t)	1; hole in tree	outward hover-glean	local; no. to so. S.A.
Myiarchus	22	forest, woodland, scrub	18; hole in tree	outward hover-glean	N.A. through so. S.A., W.I.
Deltarhynchus	1	dry woodland (t)	1; hole in tree	unknown	southwestern Mexico

[4] Treated as subgenera by Traylor (1977).

TABLE 1 (continued)

The Genera of Tyrant Flycatchers, with Notes on Habitat, Nest Form, Foraging Behavior, and Distribution

Taxa	*No. species*	*Habitats*[1]	*Nest form*[2]	*Foraging mode*	*Distribution*[3]
"*Tyrannus*" group					
Pitangus	2	lakeshore, woods, scrub (t)	2; globular or cup	supreme generalist	N.A. through S.A. tropics
Megarhynchus	1	woodland, scrub (t)	1; shallow cup	aerial hawk, up strike	C.A. through S.A. tropics
Myiozetetes	4	woodland, edges (t)	3; globular	fruit; aerial hawk	C.A. through S.A. tropics
Conopias	4	forest canopy (t, s)	2; cup or tree hole	fruit; aerial, hover-glean	C.A., Andes, Amazonia
Myiodynastes	5	forest, woodland (t, s)	5; holes or niches	fruit; up strike, aerial	N.A. through S.A.
Legatus	1	woodland, edges (t)	1; pirates covered nests	fruit; aerial hawk	C.A. to so. S.A.
Empidonomus	2	open woodland (t)	2; shallow cup	aerial hawk	no. to so. S.A.
Tyrannopsis	1	*Mauritia* palms (t)	1; open cup	aerial hawk	Amazonia
Tyrannus	13	open country, edges (t)	10; open cup	aerial hawk	N.A. through S.A. tropics, W.I.
Incertae sedis					
Xenopsaris	1	streambanks (t)	1; cup	sally-glean?	local; no. and so. S.A.

[1] Letters following the habitat descriptions refer to elevational zones, where appropriate: t = tropical; s = subtropical and humid temperate in the Andes or Venezuelan tepuis; p = paramo or puna grassland.

[2] Numbers preceding nest descriptions show number of species within the genus for which the nest is known.

[3] The following abbreviations for geographic areas are used: N.A. = North America; C.A. = Central America including Mexico; S.A. = South America (so. = southern tropical but not Patagonia, no. = northern); W.I. = West Indies.

Schauensee et al. (1978), where Tudor illustrates most of the Venezuelan forms. The 63 species shown therein illustrate the extremes of variation within the subfamily. It is easy to see how the addition of the other 117 species within these limits makes the problem of identification daunting to the field observer, and even to the museum worker!

Form and feeding specializations among the Elaeniinae are comparatively restricted. No species have the especially long wings, exaggerated tails, or short legs usually associated with the flycatching or aerial hawking behavior that typifies North American flycatchers. Only one genus, the antpipits (*Corythopis*), is exclusively terrestrial, with the pygmy-tyrants (*Pseudotriccus*) nearly so. Bill form varies from small, slender, and warbler-like to broad, flattened, spatulate shapes. Most species glean insect prey with short flights ("sally-glean") within dense vegetation. A few groups have become extensively frugivorous. Distribution is primarily within tropical latitudes and altitudes.

"Elaenia" group.—The most generalized, and perhaps most primitive, elaeniine flycatchers belong to the *"Elaenia"* lineage itself, 49 species in 10 genera: *Phyllomyias* through *Elaenia* (Table 1; Plate 1). This group includes most of the perch-gleaners, species that flit methodically through the vegetation to glean insects from nearby places while perched or hovering, but rarely flying out any distance to catch prey. Thus the smallest of these species resemble warblers. The major behavioral difference, however, is that most of these flycatchers also commonly eat fruit. Although casual frugivory is typical of most flycatchers, fruit is a major part of the diet for species in the genera *Phyllomyias, Phaeomyias, Myiopagis,* and *Elaenia.*

"Serpophaga" group.—The next group of genera in the Elaeniinae is a peculiar assemblage of small, rather more specialized birds, the *"Serpophaga"* lineage (33 species in 10 genera: *Mecocerculus* through *Euscarthmus;* Table 1). In contrast with the preceding group, these forms are poorly represented in the Amazonian lowlands but become diverse in Andean forests, river-edge habitats, and the open marshlands, grasslands, and scrub of southern South America. Even more than in the *"Elaenia"* assemblage, these are predominantly warbler-like species. The genera *Mecocerculus* (six species) and *Anairetes* (seven species) are virtually restricted to temperate and subtropical forests of the high Andes. They forage in vireo or warbler fashion at the edges of vegetation and also make frequent sallies into the air. Many travel in small single-species bands as well as in mixed-species flocks. *Anairetes fernandezianus,* the Juan Fernandez Tit-tyrant, is the only flycatcher to have colonized the Juan Fernandez Islands, some 650 km (400 mi) off the coast of Chile. It was recorded as abundant on the island of Masatierra in 1917 (A. W. Johnson 1967), but has not been found since and may now be the only modern flycatcher to have become extinct. Although *Anairetes* species are known as tit-tyrants, the resemblance to titmice (*Parus*) lies more in their crested appearance than in their habits (e.g. the Tufted Tit-tyrant, *A. parulus;* Plate 2).

Certainly the most striking member of the *"Serpophaga"* group, and one of the most bizarre of all flycatchers, is the Many-colored Rush-tyrant, *Tachuris rubrigastra* (Plate 1). In form it is an extreme version of the group, with a slender bill, a slight crest, and rather long legs. The legs are adapted to perching on vertical stalks of rushes and reeds, for this is a specialized, marsh-dwelling species. In color and behavior, *Tachuris* is unlike any other flycatcher: the bright red crown, blue face, red undertail coverts, and white flashes on the wings and tail present a startling harlequin pattern of color amongst dense reeds. The voice is equally peculiar, consisting of a rapid series of insect-like, unmusical "tic"s offered from midway up a reed or while the bird flies weakly over the rushes. This little gem-like creature is widely but locally distributed from coastal and temperate Andean Peru through Argentina and Chile, and in marshy lowlands from southern Brazil to Patagonia. *Tachuris* builds a nest as distinctive as its plumage: a cone of dried reeds attached along one side to a single reed and smoothed on the outside with a strange gum, giving the nest the appearance of having been cast in a mold (Figure 3e). Despite its weak, wren-like flight, *Tachuris* migrates from the southern parts of its range in the austral winter.

Among the five species of *Serpophaga* are two, the Torrent and Sooty tyrannulets (*S. cinerea* and *nigricans*) that have become specialized for streamside habitats; the former occurs in the Andes, the latter in southern Brazil and northern Argentina. This ecological move into open, wet, and marshy habitats by otherwise typical foliage-gleaning species may have given rise to the interesting subgroup of related species in the genera *Culicivora, Polystictus, Pseudocolopteryx,* and *Euscarthmus.* These nine species of tiny brownish birds are nearly restricted to the dry southern grasslands and marshes well south of Amazonia. Few flycatchers can truly be referred to as dry grassland specialists. The Sharp-tailed Tyrant (*Culicivora caudacuta;* Plate 1) is one of these, a species characterized by its peculiarly long, graduated tail composed of only ten rectrices, with stiff and decomposed barbs reminiscent of the spinetails (*Synallaxis* spp; Furnariidae). This species is extremely rare in museum collections but is locally common in southern Brazil where large expanses of tall native prairies still exist. Preliminary observations suggest that it may be unique among flycatchers because it feeds on grass and weed seeds as well as more standard insect fare. *Polystictus* consists of two species much like *Culicivora* in habits and plumage color, but with normal tails.

The distributions of the doraditos (*Pseudocolopteryx*) suggest how some northerly populations of southern dry-country birds might have arisen. Breeding ranges of all four species center in northern or central Argentina, where these warbler-like flycatchers inhabit dense grassy marshes. The Warbling Doradito (*P. flaviventris*) reaches Patagonia and southern Chile. All species are highly migratory, especially in the southern portions of their ranges. Migration in the Crested Doradito (*P. sclateri*) is extensive, for it winters in eastern Brazil, the Guianas, and even rarely in Trinidad. Of particular interest is the fact that it at least occasionally breeds in Trinidad (ffrench 1973). Thus a northern, resident population may eventually be established as a result of long distance migration from the south, a situation similar to the establishment of breeding European Black Storks (*Ciconia nigra*) in southern Africa (McLachlan and Liversidge 1970: 46). However, most of the discontinuous ranges among open country species in South America clearly arose during drier times, when savanna was continuous through most of the continent and Amazonian forests were reduced to small local fragments. As the forests returned, the savanna species were isolated into discontinuous patches of habitat. Both species of

Euscarthmus, which are sedentary scrub-inhabiting tyrannids, show this distribution pattern, as do many other open-country flycatchers (Fitzpatrick 1981b).

"Transitional" groups.—With the next 3 genera (28 species), we return to the apparently primitive flycatcher appearance, with drab green colors, wing bars, and some facial marks. The forest-dwelling members of the genera *Mionectes, Leptopogon,* and *Phylloscartes* seem to lead morphologically and behaviorally into the large tody-tyrant assemblage to follow. The five species of *Mionectes* are among the most frugivorous flycatchers, being typical members of the mixed-species assemblages that come and go around fruiting understory trees in the dense forest. These species are also the only flycatchers known to practice the social system known as "lek" behavior, in which males display from traditional perches, copulate with several to many females at the lek, and do not participate in care of the nest or the young (Willis et al. 1978). This social system is typical of the highly frugivorous manakins (Pipridae) and cotingas (Cotingidae) of the New World, and of birds-of-paradise (Paradisaeidae) of the New Guinea region.

Both *Mionectes* and *Leptopogon* construct long pendant nests that are suspended from the tips of branches and have an enclosed nest chamber with a lateral entrance. Significantly, all tody-tyrants build nests of the same type, a uniformity that suggests some validity as a taxonomic character. Unfortunately the nests of the 19 species of *Phylloscartes* are virtually unknown, although one species (the Mottle-cheeked Tyrannulet, *P. ventralis*) has been recorded as building a partially domed cup. As is true with so many groups of flycatchers and other tropical birds, we still lack more information than we possess about even their most basic natural history.

Phylloscartes contains an interesting behavioral dichotomy. Some species (especially those formerly separated into the genus "*Pogonotriccus*") forage in an active, gnatcatcher fashion, with tail held almost horizontally and wings slightly drooped while the bird hops incessantly from perch to perch. Other species of *Phylloscartes* sit more quietly, with the tail almost vertical, while they scan surrounding vegetation for prey. These species, which resemble *Leptopogon* in behavior as well as pattern, use the upward strike method of foraging. This is the prey capture technique seemingly perfected, and certainly specialized on, by the tody-tyrants: the sallying bird flies up and strikes the insect from an overhead substrate (usually a leaf) with a rapid stroke of the bill, without hovering or pausing during the flight. This method is most typical of species possessing broad bills and well-developed rictal bristles. In *Phylloscartes* the method occurs only sporadically, along with upward hover-gleaning and some perch-gleaning.

The antpipits (*Corythopis;* Plate 1) are recent additions to the Tyrannidae. The genus was formerly considered to be half of the family "Conopophagidae" (along with *Conopophaga*) until Ames et al. (1968) showed that antipipits are merely bizarre flycatchers. The two species (probably conspecific) are completely terrestrial, and while walking along the ground in the deep forest interior, they resemble our North American Ovenbird (*Seiurus aurocapillus*). Rather than picking insects from the litter, however, the antipipits sally upward from the ground to snatch insects from leaf undersides—thus they represent terrestrial upward strikers. This is one reason they are now placed with the apparently related *Pseudotriccus* (three species) near the tody-tyrants.

"Tody-tyrant" group.—The group of 7 genera (47 species), *Myiornis* to *Todirostrum,* constitute the tody-tyrants. These are small flycatchers, with proportionately long bills and tarsi. The large genus *Todirostrum* (Plate 2) marks the extreme in these features. All species build purse-like pendant nests with side entrances. Most tody-tyrants are found in Amazonian habitats, but a few have adapted to scrub, woodland, and even subtropical forests. Foraging behavior in this assemblage is as stereotyped as in any tyrannid lineage. All species forage predominantly by upward striking within dense vegetation. Thus, except for minor differences in plumage and bill form, the birds all are remarkable replicas of one another. This may be why their ecological segregation of habitats within Amazonia is extremely well developed. At one location as many as eight different tody-tyrant species may occur together, but no two of them are in exactly the same place: one inhabits tall forest canopy, another uses dense river edge vegetation, a third is restricted to bamboo, a fourth to interior forest vine tangles, and so on.

The genus *Myiornis* contains the smallest flycatchers, including the smallest passerine bird in the world, the Short-tailed Pygmy-tyrant, *Myiornis ecaudatus* (Plate 1). Average wing length (measured from the bend of the wing to the tip of the longest primary) for all three species is less than 40 mm (1½ in.); that of *ecaudatus* is about 33 mm (1¼ in.). With almost no tail, its tiny and rounded wings, and a strange hovering style of flight in between perches, *M. ecaudatus* gives the impression of having converged on the body form and behavior of a medium-sized beetle.

Along with *Myiornis,* the genera *Lophotriccus, Atalotriccus,* and *Hemitriccus* form an extremely homogeneous group of 27 species. Besides the small body size and long bills and tarsi common to all tody-tyrants, these species share a style of vocalization unlike that of any other flycatcher group. Vocal displays are all variations on a short trill of staccato, metallic notes, usually ascending the scale. In *Lophotriccus* the trill has become loud and long, giving rise to the local name "police-whistle bird" for the Scale-crested Pygmy-tyrant (*L. pileatus*) of the Central American and Andean montane forests. The monotypic Pale-eyed Pygmy-tyrant, *Atalotriccus pilaris,* is probably related to *Lophotriccus,* but it is a scrub and dry woodland inhabitant that lacks the peculiar laterally oriented crest typical of *Lophotriccus.* Furthermore, the four outer primaries in *pilaris* are greatly reduced and narrowed, barely resembling wing feathers at all (Figure 4g). Once again, this feature tells us little about the relationships of the species, and it almost certainly functions as a sound-maker during the strange wing-buzzing display performed by *pilaris.*

Besides *Tachuris* in the "*Serpophaga*" group, the most brightly colored flycatchers belong to the tody-tyrant genus *Poecilotriccus,* a four-species assemblage recently united from three different genera. The species are linked through their unique and peculiar color pattern and their sexual dimorphism in all but one species. The anomalous plumage pattern includes a bushy, bright chestnut crown, a yellow wing stripe reminiscent of siskins (*Carduelis*), and a complete or nearly complete black breast band. All species except the Rufous-crowned Tody-tyrant (*P. ruficeps*) are rare and locally distributed allopatrically through Amazonia. One species, the White-cheeked Tody-tyrant (*P. albifacies*) was described in 1959 by E. R. Blake and was known only from the unique holotype until 1980. Its closest relative, *tricolor,* also was known from just one specimen, collected only 650 km (400 mi) from the locality for *albifacies.* Just recently, both of us were guilty of rash judgment about our colleague Blake. We questioned the validity of his species by assuming his specimen to be a mis-sexed female of *tricolor* (Fitzpatrick 1976, Traylor 1977), thus *Poecilotriccus albifacies* Blake was merged with *P. tricolor* (Berla) for a few years. Recent field work by Fitzpatrick and by parties from Louisiana State University has proved that Blake was correct after all—*albifacies* must be recognized as a full species.

The core of the tody-tyrants comprises two large genera, *Hemitriccus* and *Todirostrum,* now numbering 19 and 14 species, respectively. All *Hemitriccus* are small, brownish-to-greenish olive birds with variable striations of olive on the breast, and sometimes washed rusty about the head and throat. The bill is long and slightly spatulate but not as wide as in *Todirostrum.* One group, labeled the "brown" species group by Fitzpatrick (1976), shows classic relict distributions surrounding, but not including, Amazonia. By a charming coincidence, Fitzpatrick and O'Neill (1979) recently discovered in this relict complex a sixth species; *Hemitriccus cinnamomeipectus,* the Cinnamon-breasted Tody-tyrant, inhabits the cloud forests of isolated mountains in northern Peru, fully 4,000 km (about 2,500 mi) from its closest relative in southeastern Brazil.

The oddly shaped bills and tails of several tody-tyrants prompted early taxonomists to recognize monotypic genera that recently have been merged. The Boat-billed Tody-tyrant, *"Microcochlearius" josephinae,* is one such, a rare species of northeastern Amazonian forests with a short, extremely broad bill resembling that of the flatbills. Snethlage's Tody-tyrant, *"Snethlagea" minor,* has peculiarly open, circular nostrils. The Fork-tailed Pygmy-tyrant, *"Ceratotriccus" furcatus,* has a forked tail with only ten rectrices, all tipped white. Although these features are distinctive, we now recognize that all these species form a natural and rather homogeneous group, united under *Hemitriccus.* Probably the genus *Oncostoma,* the Bentbill, should join the throng as the only Central American representative; its sole peculiarity, besides an odd voice, is mentioned in its English name.

The spatulate bill reaches its extreme form in *Todirostrum* (Figure 2p). In several species the bill is more than one-third the wing length, with long parallel sides and an almost squared tip. Members of the genus occur in tropical scrub, open forest, mangroves, and parks, but rarely in true primary forest. They all forage with the upward strike predominating. Their vocal abilities are restricted to nasal tics and chirps, but these birds are unusual among tyrannids in having well-developed vocal duetting between a pair. The Common Tody-flycatcher (*T. cinereum;* Plate 2) is frequently seen in parks and shrubby pastures, giving an odd display: holding the wings drooped and the tail cocked vertically over the back, the bird hitches sideways along a perch, uttering a series of "tic" sounds.

Slud (1964) was the first to comment on a common ecological feature among species of *Todirostrum.* In Costa Rica he found *T. sylvia,* the Slate-headed Tody-flycatcher, in various habitats lacking *T. cinereum,* but it was restricted to dry thorny scrub in any region containing *cinereum.* This sharp, easily observable habitat separation typifies the genus throughout the Neotropics. Terborgh and Weske (1969) mentioned seeing it among three species in eastern Peru. Haverschmidt (1968) refers to the same phenomenon in other *Todirostrum* species in Surinam. Indeed, even the geographic ranges of the species show their ecological incompatibility because many of the sister species meet without overlapping along broad distributional borders (Fitzpatrick 1976). This pattern probably stems from the remarkably similar and stereotyped foraging patterns that characterize the group.

"Flatbill" group.—The remaining lineage of 18 species in 5 genera of elaeniine flycatchers includes the flatbills and spadebills, genera *Cnipodectes* to *Platyrinchus.* Like the tody-tyrants, all feed by using the upward strike almost exclusively. The bill, like a small spoon, is used to scoop insect prey from leaf undersides. T. Sherry (pers. comm.) has discovered a remarkable ecological pattern in several of these species: they feed almost exclusively on leafhoppers, the Fulgoroidea (Homoptera). Few other groups of foliage-gleaning birds are so restricted to one taxon of insect.

The Brownish Flycatcher (*Cnipodectes subbrunneus*) might better be known by its older, more imaginative name of "Twistwing" because the strange, rotated outer primaries of the fully adult male are its most distinctive feature (certainly there are plenty of flycatchers that are brownish!). As carefully described by Zimmer (1939), the basal portion of the primary shaft is uniquely stiffened, causing the distal portion to curve upward and outward. Further, the outer portion of the feather webbing flares upward owing to a weakening in the barbs. The function of this peculiar configuration remains a mystery, but almost certainly it involves display.

Ramphotrigon, Rhynchocyclus, and *Tolmomyias* are all similar in appearance; their bills are stout, flattened, and swollen into "shovels"; and they are birds of the primary forest understory and subcanopy. The first of these genera contains three species, two of which (*megacephala* and *fuscicauda*) were until recently considered extremely rare. The seeming rarity is now known to result from extreme habitat specialization. *Ramphotrigon megacephala,* the Large-headed Flatbill, is restricted to dense canebrakes and bamboo thickets where it sings a plaintive "coo-koo"; it turns out to be rather common locally. The Dusky-tailed Flatbill, *R. fuscicauda,* inhabits vine tangles and dense, usually swampy, broken forest openings. These habitats are difficult to explore and are extremely patchy by nature. Any species restricted to them can appear to us to be rare simply because the birds were overlooked during the earlier days of collecting.

Tolmomyias resembles a miniature *Rhynchocyclus* and these genera always have been allied within the family. Ames (1971), however, found the syringes to be so different that he seriously questioned the reliability of external similarities, especially bill shape, in determining relationships in the group. This is an important observation because convergence apparently has been common within big families like the Tyrannidae. In the case just mentioned, Skutch (1960) also points out differences in mating behavior, egg color, and nest form between these two genera. Their close physical resemblance may belie their true phylogenetic relationships, having resulted from the common use of the upward strike as a foraging method, a technique that appears closely associated with the development of broad bills.

No flycatcher bills are relatively any broader than those in the genus *Platyrinchus,* the true spadebills (Plates 1 and 2). Available information indicates that these are the most stereotyped upward strikers of all, and this has been suggested as the reason for the peculiarly broad flattened bill in the genus (Fitzpatrick 1978). However, the aforementioned information from T. Sherry includes the White-throated Spadebill (*P. mystaceus;* Plate 2) as a specialist in feeding on leafhoppers (the fulgoroid Homoptera). This specialization probably acts to favor selectively the spade-shaped bill in this and the other flatbill genera. Remarkable variability in wing form also characterizes this otherwise homogeneous genus, but we cannot yet interpret its significance. Except for *P. mystaceus,* which occupies drier woodlands and subtropical forests, members of the genus *Platyrinchus* are denizens of the dark interior of primary forest. Several have insect-like songs that are barely audible to humans. Spadebills can perch for several minutes in one spot while searching for prey above them, and so are relatively difficult to see.

Fluvicolinae

The 122 species in the Fluvicolinae are by far the most widely varied group in size, form, and habits; practically all the variations and adaptations within the family as a whole occur at least once in this subfamily. Two main lineages form the bulk of the Fluvicolinae. The first consists of forest and woodland forms, most of which are sally-gleaners and hawkers within the dark interiors or open edges of tall forest. The second includes a wide diversity of forms whose center of radiation has been the dry open country south of Amazonia and the temperate grassland of the southern Andes (Smith and Vuilleumier 1971). Despite its ecological and morphological diversity, the subfamily Fluvicolinae appears to be a well-defined, closely related group on the basis of several cranial and syringeal characters (Warter 1965, Ames 1971). This relationship allows us to examine with greater-than-usual detail some of the behavioral and morphological pathways by which such a large lineage evolved (Fitzpatrick 1978).

"Myiobius" group.—The subfamily begins with a transitional group of four genera (6 species) including a peculiar monotypic form that is among the most spectacular of flycatchers. The Royal Flycatcher (*Onychorhynchus coronatus;* Plate 1) is a slender, buffy-brown flycatcher with unusually short legs and a very long flattened bill like that of a giant tody-tyrant. Its remarkable rictal bristles, the longest in the family, reach the tip of the oversized bill. The feature for which this bird is best known, however, is its elongated and fan-shaped crest, bright scarlet in the male, yellowish orange in the female, with each feather tipped with iridescent violet-blue. The crest features in a bizarre and unique display: the feathers are erected into a full semicircle around the head (Plate 1); the bill is opened wide to reveal a bright orange mouth lining; and the head is rotated about the axis of the neck, alternately in one direction and then the other, in a very deliberate mechanical fashion, giving every appearance of a wind-up toy. Presumably this display is associated with courtship, territorial encounters, or antipredator behavior, but virtually all observations have been made by collectors or mist-netters who threatened the bird with bodily harm. To our knowledge, only one ornithologist, S. Hilty, has observed the display in the wild; he saw two birds (sexes not distinguishable) performing it while facing each other on nearby perches in southern Mexico (pers. comm.). Royal Flycatcher displays are perhaps best known from their depictions on South American postage stamps!

Terenotriccus, Myiobius, and *Myiotriccus* are active, forest understory species characterized by exceptionally long rictal bristles. In the Ruddy-tailed Flycatcher, *Terenotriccus erythrurus,* the bristles reach well beyond the tip of the short broad bill. All three species of *Myiobius* practice a peculiar mode of foraging reminiscent of the American Redstart, *Setophaga ruticilla.* The broad full tail is spread horizontally, and the wings are held out from the body. The foraging individual rarely stops on a perch for more than a few seconds, twitching constantly and fanning the tail. Often the sallies after prey begin by knocking an insect off a leaf, followed by rapid aerial chases through the open understory. *Terenotriccus, Myiobius,* and *Onychorhynchus* build long pendant nests; that of *Onychorhynchus* (Figure 31) may reach a length of almost 2 m (6 ft).

The Ornate Flycatcher, *Myiotriccus ornatus,* is one of the most beautiful flycatchers, with a black head, bright yellow crest, chestnut tail, and egg-yolk-yellow rump tufts and underparts (Plate 2). An enclosed perch hawker, the Ornate Flycatcher frequents moist, tree-fern-laden ravines of the subtropical Andean forests. Like the previous genera, *Myiotriccus* commonly joins foraging flocks of mixed species whose presence it gives away through incessant uttering of a loud "pyip" call.

"Empidonax" and "transitional" groups.—In this assemblage of 12 genera (49 species), *Myiophobus* is particularly interesting because most of its species have restricted distributions. Eight of the nine species are confined to the subtropical zone of the Andes or the isolated mountains (tepuis) of southern Venezuela. Only three species have an unequivocally continuous

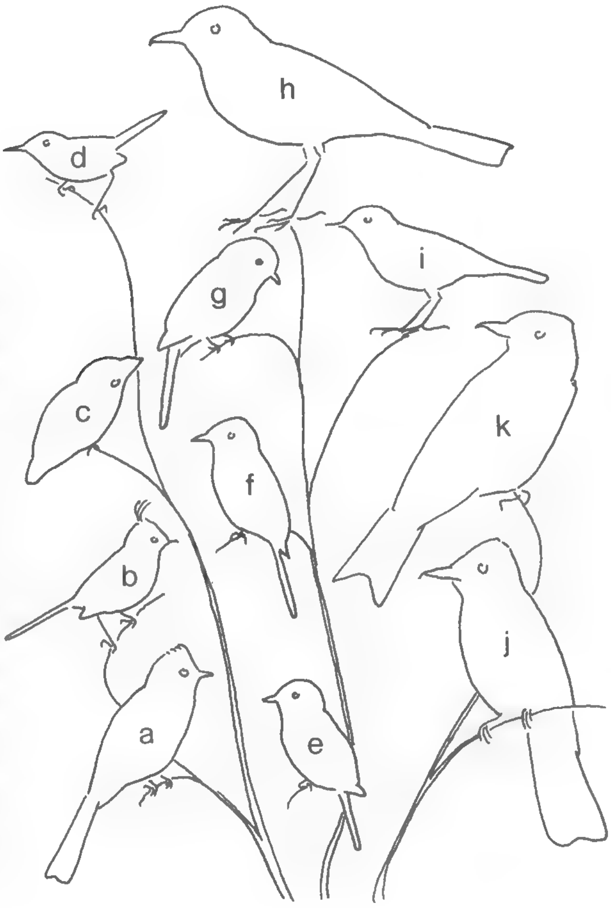
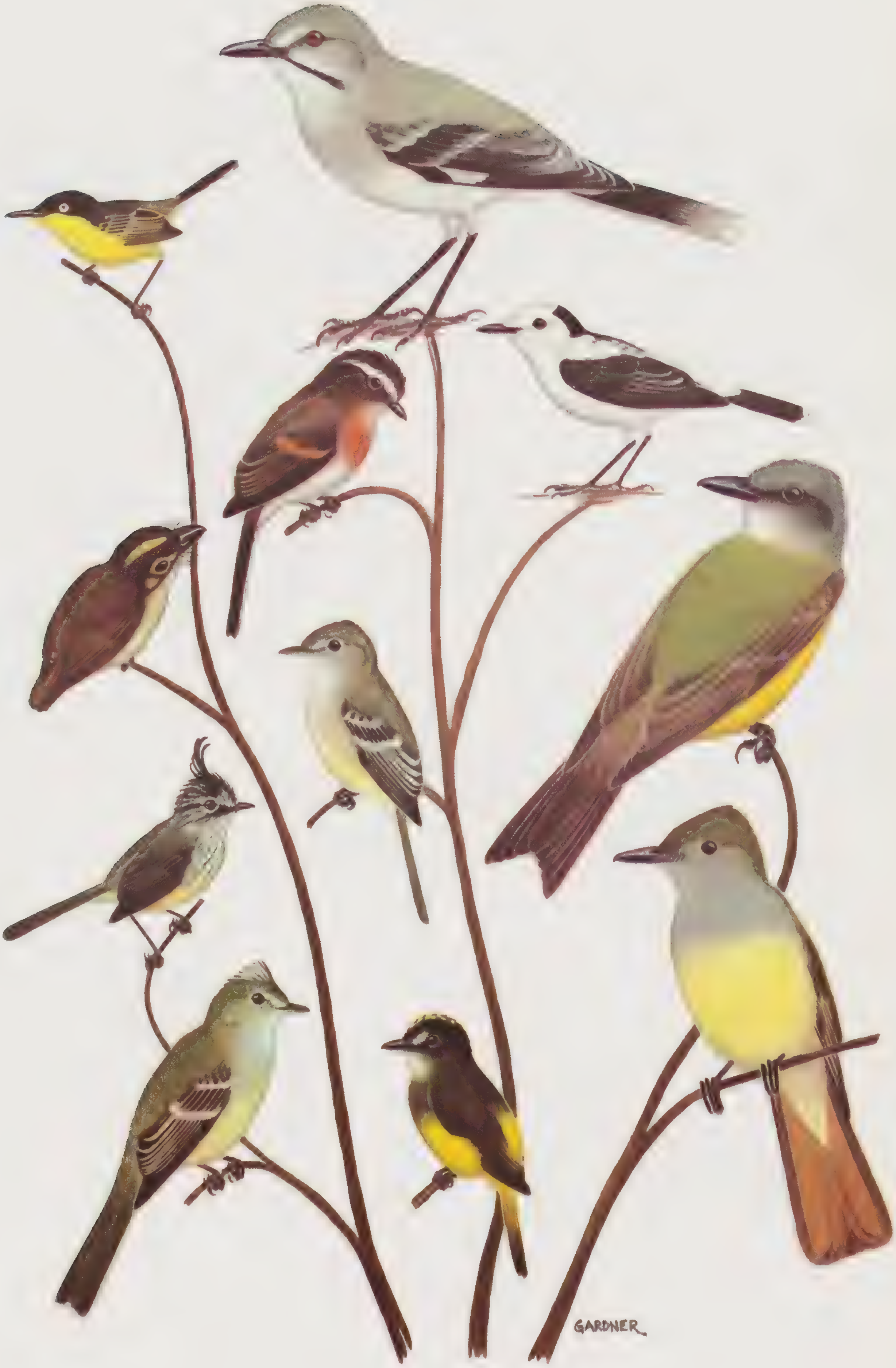


Plate 2. The three subfamilies of flycatchers, with examples of the main groups or lineages. Elaeniinae: *"Elaenia"* group (a) White-crested Elaenia, *Elaenia albiceps; "Serpophaga"* group (b) Tufted Tit-tyrant, *Anairetes parulus;* "flatbill" group (c) White-throated Spadebill, *Platyrinchus mystaceus;* "tody-tyrant" group (d) Common Tody-flycatcher, *Todirostrum cinereum.* Fluvicolinae: *"Myiobius"* group (e) Ornate Flycatcher, *Myiotriccus ornatus; "Empidonax"* group (f) Alder Flycatcher, *Empidonax alnorum;* "ground-tyrant" group (g) Rufous-breasted Chat-tyrant, *Ochthoeca rufipectoralis;* (h) Gray Monjita, *Xolmis cinerea; "Fluvicola"* group (i) Pied Water-tyrant, *Fluvicola pica.* Tyranninae: *"Myiarchus"* group (j) Great Crested Flycatcher, *Myiarchus crinitus; "Tyrannus"* group (k) Tropical Kingbird, *Tyrannus melancholicus.* Painting by Dana Gardner.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range of more than about 650 km (400 mi). Wide disjunctions characterize several of the forms; *M. roraimae,* the Roraiman Flycatcher, for example, is known from southern Venezuela, two mountains in central Peru, and a small region of southeastern Peru. As shown by Terborgh (1971), altitudinal segregation is sharply defined among members of this genus, such that as many as four species may occur on the same mountain slope but no two of them at the same altitude. The narrowness of some of these altitudinal zones probably explains why some of the species become extinct in certain areas, and why most species are rare in collections. Perhaps their distributions will emerge as more continuous once the remote eastern Andean slopes have been sufficiently explored.

In contrast to the subtropical species, *Myiophobus fasciatus* (the Bran-colored Flycatcher) occupies tropical woodland and brush from Costa Rica to Argentina. Like its rarer relatives, it forages with aerial hawking and sally-gleaning within dense vegetation, especially near openings and edges. Its close relationship to other species included in *Myiophobus* is open to doubt.

The remaining genera in this lineage, *Aphanotriccus* through *Pyrocephalus* (Table 1), contain some North American and Central American radiations, including our familiar pewees, empidonaces, and phoebes. Several Central American endemics and wide-ranging South American forms are also included. All species are similar in form to the North American representatives. They are small-to-medium sized, upright-perching, large-headed flycatchers that forage predominantly by aerial hawking either in the open or in enclosed vegetation. Most species feed at lower levels in open woodland; a few venture into open situations, and these invariably forage near the ground (e.g. *Sayornis,* phoebes; *Pyrocephalus,* the Vermilion Flycatcher).

In *Aphanotriccus* and *Xenotriccus* we find four species of highly restricted range, virtually all in Central America. Apparently these species behave more or less like typical *Empidonax,* but very little is known of their habits. *Xenotriccus* contains two species restricted to arid brush in the highlands of southern Mexico, and *Aphanotriccus* contains two even more localized forms farther south.

Mitrephanes, Pyrrhomyias, and *Contopus* form a closely related assemblage that has become specialized for aerial hawking, to the virtual exclusion of other prey capture styles. The first two genera are typical inhabitants of openings, cliff edges, and high ravines within subtropical forests from western Mexico (*Mitrephanes* only) to northern Argentina (*Pyrrhomyias* only). For hours, and even days on end, these little rufous birds sally into the open air near moist vegetation and return to the same perch, often calling incessantly. The Cinnamon Flycatcher, *Pyrrhomyias cinnamomea,* has a classic subtropical distribution, about 5,800 km (3,600 mi) long and "a mile wide" (Chapman 1926: 90) along the moist Andean slopes between 1,000 and 2,500 m (3,300–8,200 ft) in elevation, from coastal Venezuela to northern Argentina.

Fitzpatrick believes that the peculiar Cliff Flycatcher, *Hirundinea ferruginea* (Plate 1), is most closely related to *Pyrrhomyias.* The two genera share similar and unusual rufous wing patterns, calls, and "pinched" bill tips; and both build the same style of nest. Furthermore, the peculiar swallow-like proportions of *Hirundinea* (tiny short tarsi and long pointed wings) make sense in light of the species' unparalleled specialization on aerial hawking from perches on cliff faces; this morphology is easily achieved from a *Pyrrhomyias*-like ancestor. Traylor, in a spirit of amicable disagreement, prefers *Hirundinea* in the next major lineage, the true fluvicolines.

Now we arrive at the first of only three assemblages whose main radiation has occurred in North and Central America. The pewees, genus *Contopus,* have six species in that area, and only three or four in South America. They represent the principal aerial hawking flycatcher of the north temperate woodlands. In addition to the North American Coues' Flycatcher and the Eastern and Western wood pewees (*C. pertinax, virens,* and *sordidulus*), the genus is now recognized to include the Olive-sided Flycatcher, formerly known as *"Nuttallornis" borealis.* Given its new generic name, its ecologically accurate specific name, and the fact that most flycatchers have olive sides, this species might better be known by the more appropriate name of "Boreal Pewee."

In *Empidonax,* ten species are North American, four are Central American, and only two are exclusively South American, although these numbers change considerably during the nonbreeding season. All three phoebes, *Sayornis,* are North American breeders. The Black Phoebe, *S. nigricans,* however, has a continuous breeding range from California south through the Andes to Tucumán, Argentina, almost 10,000 km (6,000 mi).

Speciation in *Contopus* and *Empidonax* has occurred primarily through the development of social and behavioral isolating mechanisms rather than through change in structure or plumage pattern. For this reason, these birds are a problem for birdwatchers but a goldmine for evolutionary biologists studying processes of incipient speciation (N. K. Johnson 1963, 1980) or ecological competition (Hespenheide 1971, Beaver and Baldwin 1975, N. K. Johnson 1966). A recent classic case of recognition of sibling species through behavioral studies was Stein's (1958, 1963) dissection of Traill's Flycatcher into two species, *E. traillii* and *E. alnorum,* the Willow and Alder (Plate 2) flycatchers. Stein showed that individual birds would sing only one of two known song-types ("fitz-bew" or "fee-bee-o"), and that birds of each type failed to respond to songs of the other. He also found habitat, nesting, and distributional differences between birds of known song-type; only slight color differences were discernible between large series of each. Their plumages are so alike, however, that it is still impossible to identify individual specimens of unknown song-type from their broad overlapping ranges in central North America. Birdbanders in this area are still constrained to identify them collectively as "Traill's" Flycatcher because a bird in the hand, or the mist net, seldom sings! It remains unknown exactly why plumage pattern is so conservative in many flycatcher genera (e.g. *Empidonax, Myiarchus, Elaenia*), but the problem certainly presents major challenges to the biologist as well as the birdwatcher.

The remaining North American member of this group is the Vermilion Flycatcher, *Pyrocephalus rubinus* (Plate 1), the most brightly colored member of the entire family. This striking species also has an enormous range, from southwestern United States to northern Patagonia, but it is only a nonbreeding migrant in large areas of Amazonian South America and is missing in southern Central America. The male, with its brilliant vermilion crown and underparts, is a joy to behold on any birding day (except around Lima, Peru, where one of two local color phases is a solid sooty brown, with no trace of red). The species is similar to the phoebes in behavior, generally preferring open areas, especially near water, and frequently sallying to the ground. This is one of only two flycatchers to have reached the Galapagos Islands, where it has evolved two subspecies.

The "Ground-tyrant," *"Fluvicola,"* and allied groups.—The second major lineage within this subfamily contains those genera first called Fluvicolinae by Sclater in 1873 and kept together (in one form or another) ever since; its taxonomic treatment is by far the most stable of any tyrannid group, but in diversity of form and habits it is the least homogeneous. It is even more solidly southern South American in its radiation than the previous assemblage was North American. Of the 19 genera and 67 species in the group, only 8 and 15, respectively, occur in Venezuela, whereas 14 and 43 occur in Bolivia. The group contains the highest proportion of "strange" flycatchers in the family, including a number of monotypic genera of uncertain origin and affinities. The only generalization applicable to the assemblage as a whole is that the species prefer open habitats, even unbroken grassland and barren terrain. This preference is associated with ground-related foraging and is reflected in their speciation patterns as well as in their behavior (Fitzpatrick 1981b).

Smith and Vuilleumier (1971) present a scenario for ecological and morphological radiation among the large assemblage of chat-tyrants (*Ochthoeca;* one species is shown in Plate 2), bush-tyrants (*Myiotheretes, Xolmis*), ground-tyrants, and shrike-tyrants (*Neoxolmis, Agriornis, Muscisaxicola*). They postulate an evolutionary trend from generalized arboreal foliage-gleaners (*Ochthoeca*) of the temperate scrubs and elfin forests, through intermediates occupying open country but still perching in shrubbery (*Myiotheretes, Xolmis*), to purely terrestrial birds of steppe and even barren ground (*Muscisaxicola, Muscigralla*). This evolutionary pathway has been shown to be closely tied with gradually increasing morphological and behavioral specialization, with all the intermediate steps remarkably well preserved among modern-day species (Fitzpatrick 1978).

Ochthoeca and *Myiotheretes* are Andean genera, mostly inhabiting upper cloud forest and the stunted, mossy brush near timberline known as elfin forest. They perch on exposed twigs or outcrops, sallying into the air to vegetation or to the ground. The genus *Xolmis* (monjitas) is even more restricted to open areas and shows more reliance on perch-to-ground sallying. This genus is the major lowland assemblage, with its center of distribution in southern Brazil and Paraguay. Four of the species have broadly overlapping ranges there, and a fifth migrates to the region from southern Argentina. Intraspecific variation is slight (Vuilleumier *in* Smith and Vuilleumier 1971), and in contrast to forms like *Ochthoeca* (Fitzpatrick 1973), *Xolmis* shows relatively little range fragmentation and speciation. Many species of *Xolmis* are strikingly patterned with black and white, especially in the wings (e.g. the Gray Monjita, *X. cinerea;* Plate 2). The various harlequin patterns are dazzling and highly visible as the birds move from perch to perch with long overhead flights. The White Monjita, *Xolmis irupero,* is pure white with jet black wings. Its local name of "ghost bird" refers as much to its seeming preference for perching atop gravestones as to its ghostly plumage.

Two of the larger genera in this lineage are *Agriornis* (5 species) and *Muscisaxicola* (12), both found principally in Andean dry country above timberline, although three of the latter reach Tierra del Fuego. The genus

Agriornis, which contains the largest flycatcher species, the Great Shrike-tyrant (*A. livida*) is characterized by long, strong legs and a shrike-like bill with a severe hook at the tip. Shrike-tyrants feed on terrestrial prey, but like *Xolmis,* prefer to hunt from elevated perches, including the brick rooftops of high Andean Indian houses. The ground-tyrants (*Muscisaxicola*) are strikingly convergent on Old World chats (*Oenanthe*), being wholly terrestrial and alternately running and stopping on long slender legs as they search the ground and air for insect prey.

The remaining genera comprise a bewildering jumble of peculiar and, in large part, little-studied flycatchers, certainly the most interesting and unusual assemblage in the family. Scant evidence exists for the taxonomic affinities of most of these, except that they are fairly clearly members of this subfamily. Many are terrestrial, but apparently independently of *Muscisaxicola.* The two species of *Lessonia* inhabit bogs and forage on the ground. They are highly sexually dimorphic forms with long pipit-like hind claws. The Spectacled Tyrant, *Hymenops perspicillata* (Plate 1), is named for its unique fleshy yellow wattle around the eye. The male is jet black with large white wing patches; the female is dull brown and streaked. The Short-tailed Field-tyrant (*Muscigralla brevicauda;* Plate 1) is among the most terrestrial of flycatchers, with unusually long legs, rounded wings, and a very short tail. Its legs are so long that the scutellation extends about 10 mm *above* the tarsal joint, similar to the condition in shorebirds. The species is confined to the arid coast of Peru and Ecuador. Smith and Vuilleumier (1971) believe it to be simply an extremely derived *Muscisaxicola* offshoot. Fitzpatrick (1978) agrees, suggesting that it, like *Hirundinea,* represents a morphologically advanced specialist at the "end" of a lineage (beginning with *Ochthoeca*) that still contains species representing all the intermediate stages that preceded it.

The Cattle Tyrant, *Machetornis rixosus,* is another taxonomic enigma. In plumage it is virtually identical to kingbirds, even to its bright orange crest. Its belligerent habits and display behavior further ally it to *Tyrannus.* However, when not riding the backs of livestock in search of dislodged insects, it is strictly terrestrial, acting like a meadowlark (*Sturnella*) as much as any flycatcher. The wings are round (though the primaries are pointed) and the skull is typically fluvicoline. Further study clearly is needed to ascertain how this unusual flycatcher evolved, and from where, in the family.

Most of the remaining genera are principally aerial hawkers with black, gray, and white forming the color theme. *Knipolegus, Arundinicola,* and *Alectrurus* are sexually dimorphic; the males are black, or black and white, and the females brownish. *Fluvicola, Arundinicola,* and *Alectrurus* are grassland- and marsh-inhabiting birds. The first two (e.g. Pied Water-tyrant, *Fluvicola pica;* Plate 2) build large untidy globular nests in reeds over water. Preliminary evidence suggests that *Arundinicola* and *Alectrurus* may be polygynous breeders, with males defending territories containing several females. The peculiar aerial displays of both species of *Alectrurus,* and the extremely strange tail modifications of the males, probably are associated with the male—male competition for mates that is typical of other marsh-dwelling birds (Orians 1980). As Hudson (1920: 150) described the Cock-tailed Tyrant (*Alectrurus tricolor;* Plate 1), "the two outer tail-feathers have remarkably stout shafts, with broad coarse webs, and look like stumps of two large feathers originally intended for a bigger bird, and finally cut off near their base and given to a very small one." These feathers often are cocked up at a sharp angle, resembling a miniature rooster, hence the English name. In the Strange-tailed Tyrant (*A. risora;* Plate 1) the outer feathers of the male, and to a lesser extent the female, are greatly elongated but not in an aerodynamically strengthening fashion as in *Gubernetes* and *Muscipipra.* Instead, the shaft is bare at the base and carries a terminal pennant. Male *risora* also have the unique characteristic (within flycatchers) of entirely losing their throat feathers during the breeding season, revealing a patch of bare skin that becomes bright orange.

Colonia, Gubernetes, and *Muscipipra* are three monotypic genera, each without any obvious relatives; all three have greatly elongated tails. The Long-tailed Tyrant (*Colonia colonus;* Plate 1) has elongated central rectrices that stream out behind the bird as it sallies after aerial prey and returns to the same perch time after time. The Long-tailed Tyrant is almost never seen on any perch other than an exposed dead tree limb at forest edge. In *Gubernetes* and *Muscipipra* the tails are the more familiar "scissor" type, and the fork clearly serves to aid aerial maneuvering during long acrobatic sallies after flying prey. Both these species have the southern distributions so common throughout this lineage. *Muscipipra* apparently breeds high in the southeastern Brazilean mountains but migrates to the lowlands and becomes largely frugivorous during the austral winter.

Tyranninae

The third subfamily, Tyranninae, is morphologically much more uniform than either of the preceding. It contains 71 species of medium-to-large flycatchers, all large-headed but otherwise of normal proportions. Certainly the most familiar representatives are the kingbirds (*Tyrannus*), the only successful radiation of open-country flycatchers into North America. The subfamily contains a disproportionately large number of successful species with extensive geographic ranges, many of which extend from the United States or northern Mexico southward to central or southern South America. Much of this success results from their use of well-lighted, open habitats and forest edges; in effect they distribute themselves "over the top" of all vegetation types from desert to rain forest, thereby skirting the usual range limitations associated with habitat specialization. Many species are sympatric over much of their range, and a good lakeshore or brushy pasture in the tropics might easily contain up to ten large resident tyrannine flycatchers, most of them among the noisiest and most conspicuous birds in the area.

Two distinct lineages compose the Tyranninae, and each has a major North American component. One is the *Myiarchus* complex, including several genera that were for many years considered cotingas because of tarsal scutellation. The other lineage, *Tyrannus* and relatives, contains the kingbirds, kiskadees, and their allies.

"*Myiarchus*" group.—The present association of the genera *Attila, Casiornis, Rhytipterna,* and *Sirystes* (a total of 13 species) with *Myiarchus* (22 species) is overwhelmingly supported by anatomical evidence. This conclusion was independently reached by Ames (1971) studying syringeal structure, and by Warter (1965) studying cranial osteology. The behavior of these birds is also so like that of *Myiarchus* that even generic boundaries are questionable in some cases. The genus *Laniocera* (two species) remains in dispute. Although it has been included with the above lineage in recent treatments, current field workers familiar with its behavior and vocalizations suspect it may indeed belong in the Cotingidae, probably very close to *Laniisoma* (T. Parker pers. comm., Fitzpatrick pers. obs.).

All the recently transferred genera are forest inhabitants that hover-glean large arthropod and even vertebrate prey from dimly lit understory and subcanopy levels. They often follow mixed-species foraging flocks. The mourners, *Rhytipterna* and *Laniocera,* share with the cotingid genus *Lipaugus* (the pihas) a striking pattern of plumage variation among sister species. Each has a widespread Amazonian species east of the Andes and a closely related representative in Central America and western Colombia. In each case the Amazonian form is gray-green, and the Central American is bright rufous. This pattern is not the result of close phylogenetic relationship. The parallel plumage variation is either coincidental convergence, or possibly a case of mimicry among ecologically similar species.

Myiarchus is the largest and one of the most widespread of all flycatcher genera. Two species are wholly North American (Great Crested, *crinitus* [Plate 2], and Ash-throated, *cinerascens*); two more breed in the American southwest (Wied's Crested, *tyrannulus,* and Olivaceous, *tuberculifer*); six are strictly West Indian (the only major tyrannid radiation there); one reached the Galapagos Islands; and the rest occur from Mexico to northern Argentina. Because of remarkable similarities of plumage and structure within the genus, its taxonomy once was in disarray. Fortunately this is no longer the case, owing to the extended and meticulous field and museum studies of W. E. Lanyon (e.g. 1963, 1967, 1978). For instance, in straightening out *Myiarchus,* Lanyon demonstrated that two taxa, *panamensis* and *venezuelensis,* actually are two full species that have been "hiding" as subspecies of *ferox.* All *Myiarchus* build nests inside cavities, which they decorate with fragments of snake or lizard skin. This is so stereotyped a behavior pattern that it now serves as an important criterion for close relationship to *Myiarchus* in Lanyon's continuing studies of the other genera in this group. One of these is *Deltarhynchus,* a western Mexican endemic genus that Lanyon is now studying in the field (Lanyon in press).

"*Tyrannus*" group.—The first five genera, *Pitangus* through *Myiodynastes,* in the *Tyrannus* lineage (9 genera, 33 species), are diverse in size, form, and habits, but are bound together by a remarkably conservative plumage pattern. This is found in the Great Kiskadee (*Pitangus sulphuratus*) that reaches southern Texas, and in the Boat-billed Flycatcher (*Megarhynchus pitangua;* Plate 1). Basically the belly is bright yellow and the head is striped black and white. Because of the uniform plumage and the unclear boundaries between genera, the whole group could rightfully be treated as one genus.

Many of these yellow-bellied tyrannines are largely frugivorous over part or all of the year. The Piratic Flycatcher, *Legatus leucophaius,* almost certainly the most frugivorous flycatcher of all, spends most of its time sitting high above cacique and oropendola (Icteridae) colonies, calling incessantly and occasionally flying off to a fruiting tree to fill up on ripe fruit before returning to its watchpost. Its association with cacique colonies is related to its habit of forcibly appropriating the nests of the larger icterids, through continual harassment of the owner until the latter gives up and begins building another nest. The Piratic Flycatcher is a highly migratory species at both ends of its range. The bird migrates between tropical forest regions of Central America or southern South America, and southern Amazonia, apparently in response to changing availability of fruit within these regions (Morton 1977).

Besides eating fruit, most of the big tyrannines can be extremely catholic in their diet. The Boat-bill (*Megarhynchus*) may feed on large cicadas, butterflies, and arboreal lizards, capturing them with its huge bill (Plate 1). Streaked Flycatchers and relatives (*Myiodynastes*) forage in open forest canopy and understory, where they snatch prey from leaves, the air, and even the ground. No flycatcher, however, matches the Great Kiskadee (*Pitangus sulphuratus*) in foraging versatility. It is indeed the supreme generalist, taking advantage of whatever local source of large food items it can find, including fish, lizards, frogs, tadpoles, baby birds, all manner of fleshy fruits, millipedes, large beetles, carrion, even garbage. This kiskadee generally frequents the water's edge, where it hunts in kingfisher fashion, but it can also be the most common species in city parks or desert scrub.

The genus *Tyrannus* includes our familiar kingbirds as well as the Scissor-tailed (*T. forficata*) and Fork-tailed (*T. savana*) flycatchers, formerly separated into their own genus on the basis of their long forked tails. *Tyrannus* occurs from northern British Columbia to southern Argentina and throughout the West Indies, making this the most widespread genus of flycatchers. The center of radiation appears to have been North America, with eight species breeding at least marginally within the United States (including the Tropical Kingbird, *T. melancholicus;* Plate 2), two others endemic to the West Indies, and only two species restricted to South America.

Kingbirds are aerial hawking specialists, inhabiting open country and woodland or forest edges where they sit on exposed, often high, perches in search of flying insects. They have long pointed wings and generally forked tails; both features facilitate their powerful aerial sallies and agile maneuvers in pursuit of prey. The males of all species, and the females to a lesser degree, have the outer primaries notched in a variety of ways. The Fork-tailed Flycatcher is unique in that each of its four subspecies has a different pattern of primary notching (Figure 4m-p).

The Eastern Kingbird (*Tyrannus tyrannus*) has the most extensive migration of any flycatcher, breeding well north into Canada and wintering entirely south of the equator from western Amazonia to Argentina. On migration and on its tropical wintering grounds, the Eastern Kingbird's behavior would confuse those who know it only in summer; outside the breeding season, it travels in large, blackbird-like flocks, feeds almost exclusively on fruit, and is subordinate to all its large, tropical-resident relatives (Fitzpatrick 1980b). Apparently the wintering flocks are nomadic, descending on fruiting trees to remain for days at a time, then picking up and disappearing over the treetops to find fruit elsewhere.

The final genus, *Xenopsaris,* (one species, the White-naped Xenopsaris, *X. albinucha)* has been transferred back and forth between the flycatchers and cotingas several times. Its tarsal scutellation is a type occurring primarily in cotingas, and its glossy black cap in the male is similar to that in many *Pachyramphus* (a genus also now considered a flycatcher of sorts); but in wing shape and nest form *Xenopsaris* is unlike the becards. Although we consider that the balance of evidence favors keeping *Xenopsaris* in the flycatchers, it has no clear relationship to any particular group and is placed at the end of the list.

SUCCESSFUL RADIATION OF THE FLYCATCHERS

Having reviewed the diversity within this dominant New World family, we return to the question raised at the outset. How and why did the tyrant flycatchers achieve their state of dominance? Unfortunately our speculations must rely entirely on present distributions (Figure 5), numbers, and ecological relationships with other birds (Figure 6), because the fossil record of passerines from South America is both poor and little-studied. Our reconstruction of the successful radiation of the flycatchers therefore must be restricted to inference and conjecture.

We can assume that at the time of separation of South America from Africa and Antarctica early in the Tertiary, the principal passerine elements were ancestors of the present non-oscine families. Today these families make up about 60 percent of the perching bird fauna of South America. Early in the evolutionary history, the ancestral forms gave rise to two major independent radiations within the various habitats of the Neotropics, especially in the great tropical forests. One was to evolve into the complex of families now classified as the Furnarioidea, which in turn is divided into two well-marked lineages. The first of these includes the ovenbirds, Furnariidae (215 species), and the woodcreepers, Dendrocolaptidae (48 species). They are generally strong-billed insectivorous birds, many of which gather food by probing, tearing, and actively searching hard-to-reach places such as crevices in tree trunks. Others have adapted to an astonishingly broad variety of habitats, much as flycatchers have done. One furnariid group in southern and high Andean South America paralleled the tyrannid ground tyrants by adapting to terrestrial life in open country. The other radiation within the Furnarioidea is represented by the antbirds, Formicariidae (232 species), and tapaculos, Rhinocryptidae (28 species). These are largely foliage-gleaning insectivores that gather food by actively searching and perch-gleaning, less often by probing, tearing, or sallying. They are almost exclusively forest birds, being found primarily in lowland forests (Formicariidae) or mossy cloud forests (Rhinocryptidae). In Amazonia the antbirds constitute the dominant group of insectivorous birds in the forest interior, with only a few commonly found in open or edge habitats.

The second major non-oscine lineage to radiate during the Tertiary, the Tyrannoidea, gave rise to the modern families of manakins, Pipridae (57 species), and cotingas, Cotingidae (80 species)—both of which specialized on fruit as their major food—as well as several small families and the huge family of tyrant flycatchers (374 species). The Tyrannidae probably evolved from a generalized, partially frugivorous forest bird resembling today's tyrant-like manakins (genera *Piprites, Schiffornis, Neopelma, Tyranneutes*). Many flycatchers also eat fruit, but the family achieved its success by expanding into the sallying-insectivore niche unoccupied by the Furnarioidea. Thus flycatchers could spread into virtually all habitats that contained insects (and places to sit and search for them). Their search-and-sally foraging style was suited to well-illuminated forest edges even more than to forest interior. As a result, tyrannids dominate in scrublands, forest canopies, clearings, and lake and river margins more than in the dark forest interior where furnarioids prevail. However, the success of flycatchers even as forest-dwelling birds is evident in the distribution and diversity of the family in South America (Figure 5). The highest concen-

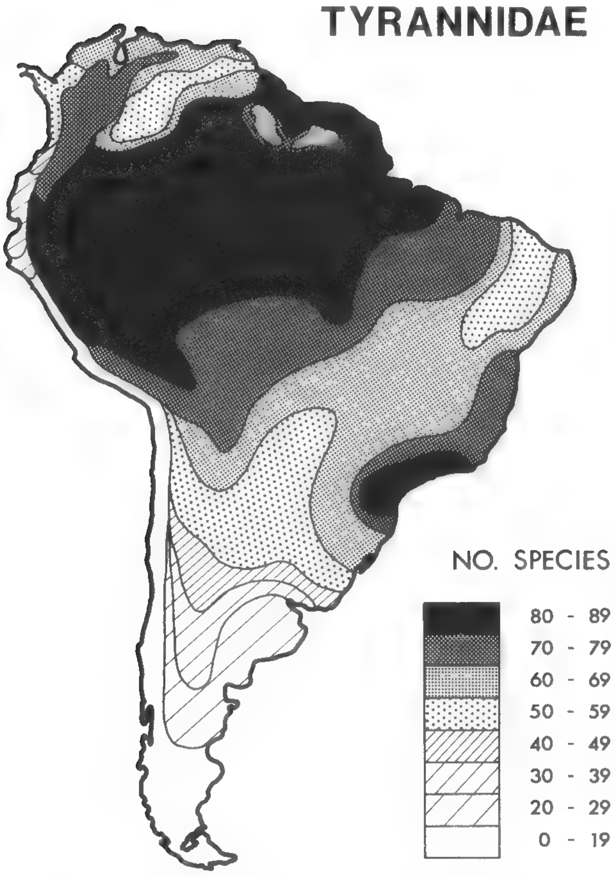

Figure 5. Numbers of sympatric flycatcher species throughout South America (breeding ranges only). From Fitzpatrick (1981b), with permission.

trations of species are in the tropical forests of Amazonia and Guiana, the coastal forests of southeastern Brazil, and in the subtropical forests of eastern Ecuador and Peru. Flycatcher diversity drops off rapidly in the drier regions, without regard to habitat or altitude.

The key to the success of the non-oscine radiation was the isolation enjoyed by South America during most of the Tertiary, when there was little or no competition from the oscine families that were evolving in North America. The non-oscines effectively locked up most of the possible insectivorous niches, even in the rich, vast, and variable tropical forests. In the modern Neotropics they continue to coexist in unparalleled diversity, in part through broadly differing foraging positions and food habits (Figure 6). Although the rain forest may have provided the center of the non-oscine radiation, open woodland existed as far back as Eocene times in southern Argentina (Webb 1978). By mid-Oligocene, grassland and semi-arid savanna existed north to Bolivia. Birds could therefore adapt to these habitats quite early. Furnariids and tyrannids were the groups to invade the open country above timberline during the subsequent (and relatively recent) rise of the Andes (Vuilleumier 1969). As a result of these already established radiations, once South and North America were connected, the invading oscines could radiate widely as fruit-eaters (180 species of tanagers) or seed-eaters (189 species of finches, buntings, and grosbeaks), but the generally insectivorous families were more limited by competition (only 33 warblers, 21 vireos, 57 blackbirds, 38 wrens, and 28 thrushes in South America).

Although prolonged evolution in the absence of competition from other groups can explain the success of the non-oscines as a whole, the particular success of the flycatchers demands further explanation. The full story is not yet understood and is the subject of continuing study. A few general patterns are clear, however, and they probably account for much of the tyrannid success. Flycatchers are capable of using virtually all land habitats, principally because their various sallying styles give them access to all leaf surfaces from treetops to the ground, in habitats ranging from forest to desert. Because they are particularly successful in exposed forest microhabitats where light intensity is high, flycatchers apparently were preadapted for expansion into scrubby and edge habitats where foliage and insect densities often would be lower than those preferred by furnarioids. By adapting to high light intensities, flycatchers were able to colonize the "outer edges" of habitats throughout the Neotropics. They are the principal salliers of interior forest as well, but this hunting style is less successful in the dim understory than in openings, canopies, and edges (Figure 6). The sallying hunting technique took flycatchers into the savanna, probably first as "bluebird-style" hunters, and later as "chats" and "pipits." Furnariids, however, took to the open country as well, especially in rocky terrain well suited for birds already built with powerful legs and probing bills. In short, while the other non-oscine families, especially the Furnariidae, showed flexibility in moving into new habitat zones, none of them began with a sufficiently versatile hunting repertoire to permit colonization of *all* these zones. (Note that even furnariids are essentially absent in the tropical forest canopy.)

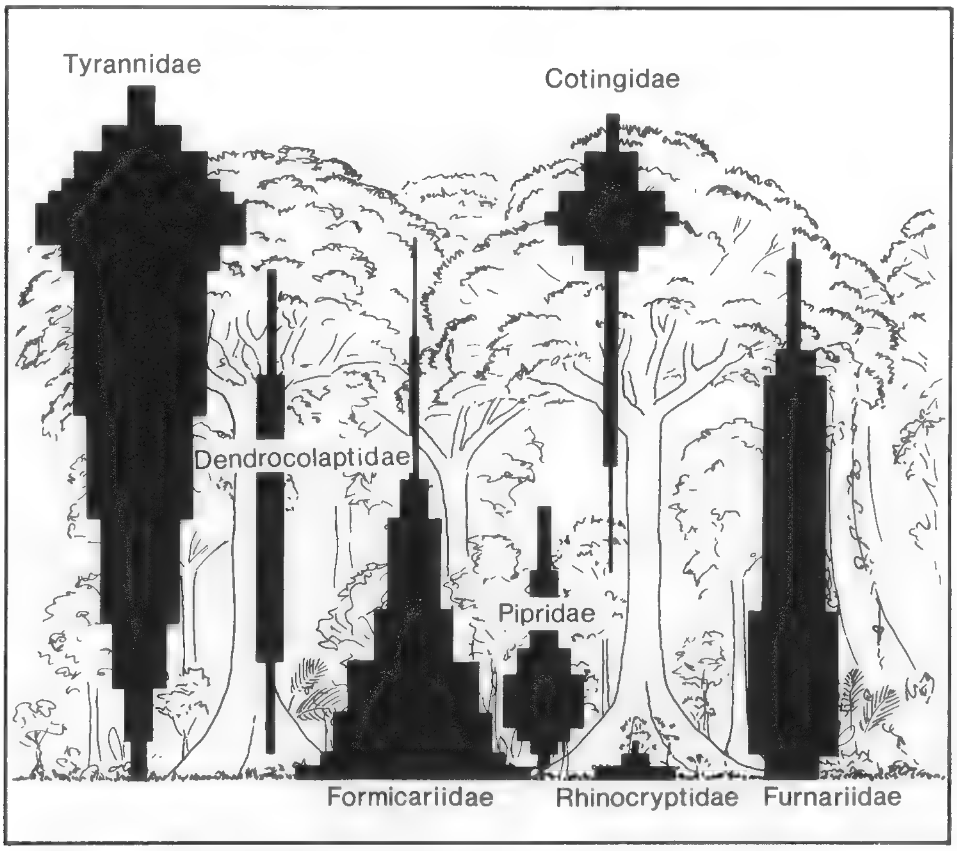

Figure 6. Relative densities and ecological positions among the six principal non-oscine families in the neotropical rain forest. Overall relative diversity for each family at each forest layer is indexed by the horizontal width of the black bar. Note that Tyrannidae is the only family represented at all heights, including the aerial feeding zone above the canopy. Flycatchers are least diverse at the forest floor, and they increase steadily toward the canopy.

A final piece of the tyrannid success story involves their invasion of North America, a feat not accomplished by any other non-oscines. The reasons, we think, parallel those just outlined for the flycatchers' success in their "home" continent—namely the ability to use almost any habitat, and the successful spread of lineages outside the tropical forest. As pointed out by Webb (1978), the great majority of vertebrates that reciprocally invaded North and South America in the late Pliocene were those inhabiting open woodland rather than forest or grassland. Woodland flycatchers such as *Empidonax, Contopus, Sayornis,* and *Myiarchus* apparently found a direct route northward through their preferred habitat. No North American resident oscine families were sallying insectivores, so that even the open-country forms like *Tyrannus* were ecologically free to move northward.

Finally, for reasons still unknown, few members of the Furnariidae and no species in the Formicariidae or Rhinocryptidae are migratory, even within the tropics. Many flycatchers are highly migratory (Fitzpatrick 1980b), and the southern South American species presumably have been migrants for millions of years. For a tropical bird group to invade the North American forests and grasslands, many of which are snowbound, leafless, and devoid of active insects or other food for half the year, the species would have to have at least some propensity and ability to go south for the winter. The strong-flying flycatchers of the aerial-sallying type possess these traits. Thus we North Americans do get an annual glimpse of the great neotropical non-oscine radiation, but it is only a glimpse. A few members of one family, the Tyrannidae, did successfully invade and even evolve in our temperate forests, where they compose the well-defined and rather restricted type of bird that North Americans know as "the flycatchers." Except for the hardy phoebes, however, even these flycatchers leave us for over half the year, to return to rich tropical habitats and join their multitudinous and varied relatives in their ancestral home.

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TABLE 2

The Genera of Tyrant Flycatchers, Showing Distribution of Warter's (1965) Cranium Types, and Ames' (1971) Syringeal Groups

		Warter				*Ames*
Taxa	*No. species*	*Species examined*	*Nasal septum types*	*Interoribital septum types*	*Palatine types*	*Groups*[1]
Subfamily **ELAENIINAE**						
"*Elaenia*" group						
Phyllomyias	10	1	1	4	?	(A)
Zimmerius	5	3	6	3	2	
Ornithion	3	1	2–3	4	1	
Camptostoma	2	1	2	4	2	A
Phaeomyias	1	1	2	2	2	A
Sublegatus	2	1	5	1	2	
Suiriri	1	1	5	2	2	A
Tyrannulus	1	1	2	3	?	A
Myiopagis	7	1	1?	3	1	A
Elaenia	17	9	5	1	1	A
"*Serpophaga*" group						
Mecocerculus	6	1	5	4	1(2)	H
Serpophaga	5	3	5	4	2	H
Inezia	3	1	5	4(3)	2(1)	
Stigmatura	2	1	2	4	2	
Anairetes	7	2	5	4	2	H
Tachuris	1	1	?	4	2	
Culicivora	1					
Polystictus	2	1	6	3	2(1)	
Pseudocolopteryx	4	1	2?	4	1(2)	
Euscarthmus	2					

TABLE 2 (continued)

The Genera of Tyrant Flycatchers, Showing Distribution of Warter's (1965) Cranium Types, and Ames' (1971) Syringeal Groups

Taxa	*No. species*	*Warter*				*Ames*
		Species examined	*Nasal septum types*	*Interoribital septum types*	*Palatine types*	*Groups*[1]
"Transitional" groups						
Mionectes	5	3	5?	4	1?	
Leptopogon	4	2	3	4	1	
Phylloscartes	19	5	1, 2?, 3?	4	2	
Pseudotriccus	3					
Corythopis	2					
"Tody-tyrant" group						
Myiornis	3	1	1	4	2	B
Lophotriccus	4	2	2, ?	4	2	B
Atalotriccus	1					
Poecilotriccus	4					
Oncostoma	2	1	1	4	1	B
Hemitriccus	19	2	1,1?	4	1,2	B
Todirostrum	14	4	2	4	2	
"Flatbill" group						
Cnipodectes	1	1	1(3)	4	1(2)	
Ramphotrigon	3					
Rhynchocyclus	3	2	1(3)	4	2(3)	
Tolmomyias	4	2	1(3)	4	1	
Platyrinchus	7	3	3	4	3	(B)

TABLE 2 (continued)

The Genera of Tyrant Flycatchers, Showing Distribution of Warter's (1965) Cranium Types, and Ames' (1971) Syringeal Groups

		Warter				*Ames*
Taxa	*No. species*	*Species examined*	*Nasal septum types*	*Interoribital septum types*	*Palatine types*	*Groups*[1]
Subfamily **FLUVICOLINAE**						
"*Myiobius*" group						
Onychorhynchus	1	1	1	3	1	C
Myiotriccus	1					
Terenotriccus	1	1	6?	2	3	C
Myiobius	3	3	6	1	3	C
"*Empidonax*" group						
Myiophobus	9	1	6	4?(1)	2	(F)
Aphanotriccus	2					D
Xenotriccus	2	1	6	2	3	D
Hirundinea	1					
Pyrrhomyias	1	1	6	4?(1)	3	C
Mitrephanes	2	1	6	2	3	(D)
Contopus	10	8	6	1	3 (once 2)	D
Empidonax	16	10	6	2	3	D
Nesotriccus	1	1	2	4?	1	
Cnemotriccus	1	1	6	2	2	
"Transitional" group						
Sayornis	3	3	6	2	3	D
Pyrocephalus	1	1	6	2	2(3?)	

TABLE 2 (continued)

The Genera of Tyrant Flycatchers, Showing Distribution of Warter's (1965) Cranium Types, and Ames' (1971) Syringeal Groups

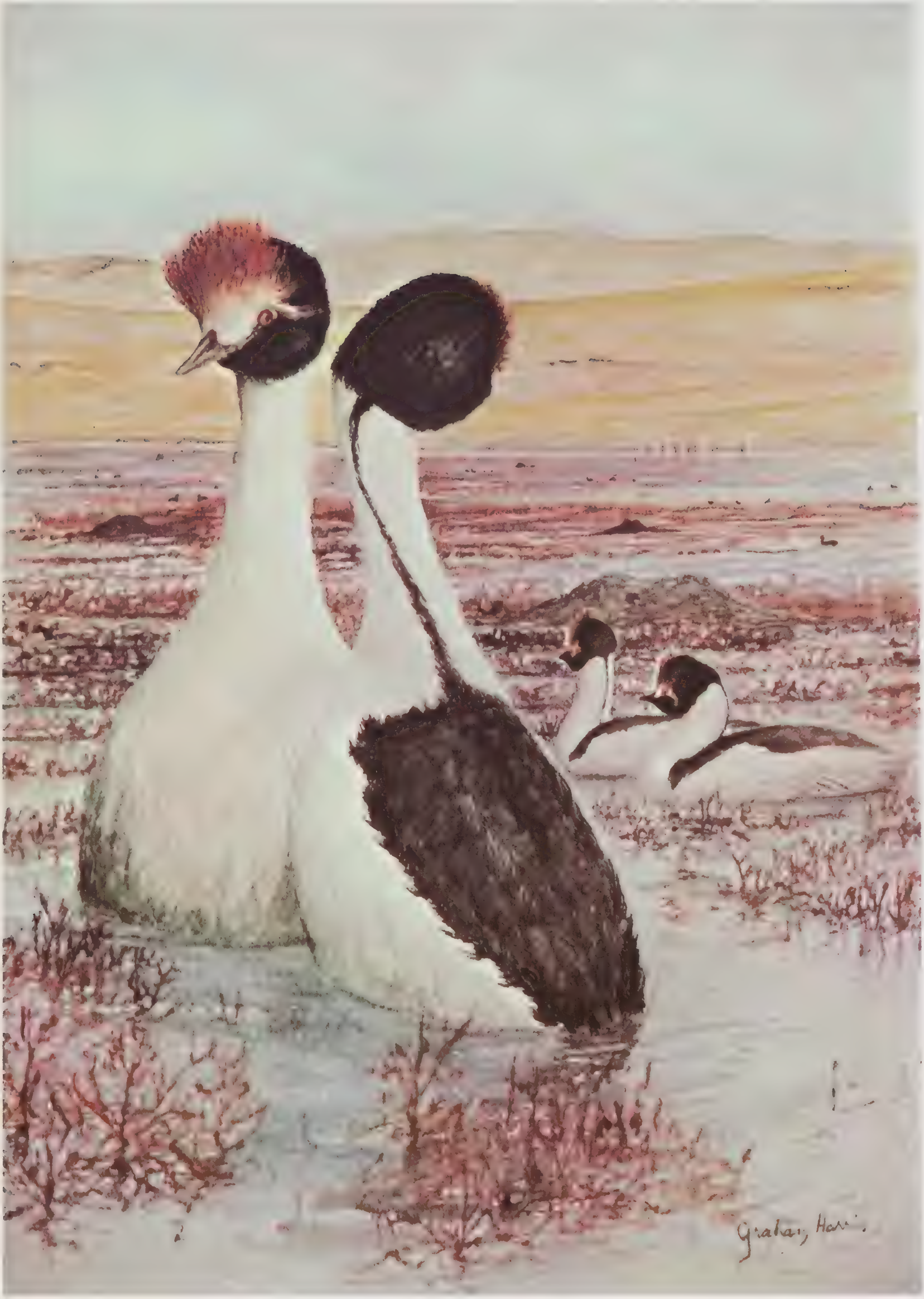
Taxa	*No. species*	*Warter*				*Ames*
		Species examined	*Nasal septum types*	*Interoribital septum types*	*Palatine types*	*Groups*[1]
"Ground-tyrant" group						
Ochthoeca	11	5	6	2	2 (once 1)	
Myiotheretes	6	1	6	?	1	
Xolmis	6	6	6	2	1	E
Neoxolmis	2	1	6	2	1	E
Agriornis	5	3	6	2	1	E
Muscisaxicola	12	3	6	2	1	E
Muscigralla	1	1	5	2	1	D?
"*Fluvicola*" group						
Lessonia	2	1	6	3	2	(E)
Knipolegus	10	2	6	2	1	E
Hymenops	1	1	6	3	2	(E)
Fluvicola	2	1	6	3	2	E
Arundinicola	1	1	6	3	1	
Colonia	1	1	6	1(4)	2	
Alectrurus	2	1	6	1(4)	1	
Gubernetes	1	1	6	1	1	E
Uncertain affinities						
Satrapa	1	1	6	3	2	(E)
Tumbezia	1					
Machetornis	1	1	6	2	2	
Muscipipra	1					E

TABLE 2 (continued)

The Genera of Tyrant Flycatchers, Showing Distribution of Warter's (1965) Cranium Types, and Ames' (1971) Syringeal Groups

Taxa	*No. species*	*Warter*				*Ames*
		Species examined	*Nasal septum types*	*Interoribital septum types*	*Palatine types*	*Groups*[1]
Subfamily **TYRANNINAE**						
"*Myiarchus*" group						
Attila	7					F
Casiornis	2					F
Rhytipterna	3	2	2	1	1	F
Laniocera	2					F
Sirystes	1	1	2	1	1	(E)
Myiarchus	22	11	2	1	1	F
Deltarhynchus	1					
"*Tyrannus*" group						
Pitangus	2	2	1	1	1	G (only *sulphuratus*)
Megarhynchus	1	1	1	1	1	G
Myiozetetes	4	3	1	1	1	
Conopias	4	1	1	1	1	G
Myiodynastes	5	3	1	1	1	G
Legatus	1	1	2	1	1	
Empidonomus	2	2	1	1	1	G
Tyrannopsis	1	1	1	1	1	G
Tyrannus	13	7	1	1	1	G
Incertae sedis						
Xenopsaris	1					

[1] A. Elaenia group; B. Colopteryx group; C. Myiobius group; D. Nuttallornis group; E. Fluvicola group; F. Myiarchus group; G. Tyrannus group; H. "alike," but not a group; ( ) "related," but not part of a group.


Graham Harris

THE HOODED GREBE ON LAGUNA DE LOS ESCARCHADOS: ECOLOGY AND BEHAVIOR

ROBERT W. STORER

Southern Patagonia in southernmost South America is dominated physically and climatically by the Andean Cordillera de Darwin. In this region the "roaring forties" give way to the "furious fifties." These west winds drop most of their abundant moisture on the temperate rain forests of the western Chilean slopes and higher parts of the mountains, leaving a deep rain shadow over the Argentinian plain that slopes gradually from the eastern foothills to the Atlantic. Much of the moisture from these westerlies collects in vast glaciers that end in a series of large lakes drained by rivers meandering through valleys cut into the arid plain. The southernmost of these lakes, Lago Viedma and Lago Argentino, empty into the Río Santa Cruz, which carries their milky, turquoise-blue glacial water across 350 km (217 miles) of desert to the Atlantic.

It was up this river that Charles Darwin and the crew of H.M.S. *Beagle* hauled longboats in April and May of 1834. Had Darwin climbed the escarpment to the south of the point at which the expedition turned back, and had he proceeded a few kilometers onto the plain, he might have found the Laguna de Los Escarchados and a grebe that was not discovered by scientists until 140 years later. But the party's food supplies were low, and "the appearance of the country offered no temptation to proceed any further," so the expedition returned to the *Beagle* (Darwin 1888: 229).

On 27 April 1974 Maurice Rumboll and Edward Shaw visited this lake, and Rumboll collected a grebe to teach Shaw how to prepare a study skin. When the specimen was brought back to the Museo Argentino de Ciencias Naturales in Buenos Aires, it was found to represent a new species, which Rumboll described as *Podiceps gallardoi,* the Hooded Grebe or Macá Tobiano (1974). With the aid of a grant from the National Geographic Society, I was able to visit the Laguna de Los Escarchados to study the ecology and behavior of this remarkable bird. The spectacular courtship behavior of many grebes provides valuable information about relationships within the grebe family; ecological information can help define habitat requirements important in looking for other populations of rare species and in aiding efforts to save them from possible extinction.

Plate 1. Hooded Grebe, *Podiceps gallardoi*. Painting courtesy of Maurice Rumboll.

ITINERARY AND METHODS

James D. Hammond and I reached Río Gallegos, Argentina, by air on 27 December 1975. The following day we drove with Maurice Rumboll and Miguel Hinrichsen to Calafate, stopping at Laguna de Los Escarchados en route. We made our headquarters at Calafate and from there visited Los Escarchados for 14 days between 29 December and 19 January 1976. Rumboll left Calafate on 11 January and the rest of us on 20 January. We searched other areas in vain for Hooded Grebes on 5 and 15 January, and on 17 January made an aerial search for lakes suitable for the grebe. Limnological data and plankton samples were taken from Los Escarchados on two days. Rumboll collected two Hooded Grebes and one hybrid between that species and the Silver Grebe, *Podiceps occipitalis* (Storer in press). Stomach contents of these and one other Hooded Grebe taken earlier by Rumboll were analyzed. One specimen was preserved in formalin after the skin was removed.

Behavioral observations were augmented by tape recordings and cine film, the latter studied on a film analyzer. The holotype and a second specimen were studied and measured in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," in Buenos Aires.

THE LAKE

Laguna de Los Escarchados is approximately 3 km (1.9 mi) long and lies at an elevation of some 700 m (2,300 ft) on the plateau south of the Río Santa Cruz valley, about 70 km (43 mi) east-southeast of Calafate. It lies west of the main road between Calafate and Río Gallegos, a few kilometers after the road climbs out of the valley and onto the plateau. This upland country is dominated by bunch grass, heavily grazed by sheep, and interspersed with very short, spreading, or even rock-encrusting flowering plants of a considerable variety. The flowers of these plants are often conspicuous because of their large size in relation to the rest of the plant, or because of the groups of small flowers that bloom simultaneously. The lake water is derived from snow melt, and is clear and slightly alkaline. The principal aquatic plants in the lake are a milfoil, *Myriophyllum elatinoides* Gaud., which covers more than one-half of the lake's surface, and a globular alga up to 25 mm (1 in.) in diameter; masses of the latter are blown ashore and form dried mats along the eastern shore of the lake. The emergent portion of the *Myriophyllum* is deep carmine. This creates masses of intense color that with the almost black-blue of the wind-ruffled clear water, contrast vividly with the drab tans of the rest of the landscape. The submerged parts of the *Myriophyllum* are green, and when piled onto nest platforms by coots and grebes, are conspicuous against the red of the emergent parts. In some places grasses or sedges grow near the water, but these are grazed by sheep and Upland Geese (*Chloephaga picta*). With seasonal fluctuations in water level, littoral vegetation has little opportunity to develop. There is thus a band of open water between the *Myriophyllum* beds and the shore, and here the grebes often forage.

No one writing of the lake could fail to mention the wind, which blows almost constantly; on at least two of our visits to the lake, the wind gusted to over 100 km (60 miles) per hour. Aside from the wind's direct effect on the birds, it hastens evaporation and accelerates the lowering of the lake level through the dry summer. According to Rumboll, the lake freezes over in winter and the birds leave.

We found no evidence of fish in the lake and doubt that there are any. On the other hand, plankton was abundant. Large and small calanid copepods, daphnias, and ostracods teemed. Two snails, *Lymnaea diaphana* King and *Succinea burmeisteri* Doering; leeches; dytiscid beetles; and chironomid flies (*Psectrocladius* sp.) were common.

Two wide-spread temperate South American grebes were also present on the lake: a flock of about 30 Silver Grebes (*Podiceps occipitalis*), a highly gregarious relative of the Eared Grebe (*P. nigricollis*), and several White-tufted Grebes (*Rollandia rolland*), a less gregarious species. We found many other water birds on the lake, including Chilean Flamingos (*Phoenicopterus chilensis*), Black-necked Swans (*Cygnus melanocoryphus*), Coscoroba Swans (*Coscoroba coscoroba*), Upland Geese (*Chloephaga picta*), Flying Steamer-ducks (*Tachyeres patachonicus*), Chiloe Wigeons (*Anas sibilatrix*), Yellow-billed Teal (*A. flavirostris*), Crested Ducks (*A. specularioides*), Brown Pintails (*A. georgica*), Red Shovellers (*A. platalea*), Red-gartered Coots (*Fulica armillata*), White-winged Coots (*F. leucoptera*), Wilson's Phalaropes (*Phalaropus tricolor*), and Kelp Gulls (*Larus dominicanus*). Of these, only the steamer-ducks and Red-gartered Coots were nesting during our visit. Buff-necked Ibises (*Theristicus caudatus*) and waders, including Fuegian Oystercatchers (*Haematopus leucopodus*), Two-banded Plovers (*Charadrius falklandicus*), Rufous-chested Dotterels (*Zonibyx modestus*), Magellanic Plovers (*Pluvianellus socialis*), Common Snipe (*Capella gallinago*), White-rumped Sandpipers (*Calidris fuscicollis*), and Baird's Sandpipers (*C. bairdii*) were found around the edges of the lake, while Tawny-throated Dotterels (*Oreopholus ruficollis*) and Least Seedsnipe (*Thinocorus rumicivorus*) were found in the surrounding grassland. Francisco Erize (MS) reported Southern Lapwings (*Vanellus cayennensis*), Hudsonian Godwits (*Limosa haemastica*), and White-bellied Seedsnipe (*Attagis malouinus*) in addition to the species we observed.

On 1 January, we tested the water with a Tetra test kit and found a pH of 8.7–9.0; 0.00–0.05 ppm nitrites. The surface water temperature (over a depth of 1 m) was 12.5° C (54.5° F) and the air temperature 8.5° C (47.3° F). On 19 January the pH was 9.0+, a difference that might be accounted for by either evaporation or testing techniques.

THE HOODED GREBE

The Hooded Grebe is a short-necked, broad-bodied grebe (Plate 1). In its body proportions and striking black-and-white pattern, it might be compared to more narrow-bodied species such as the Western (*Aechmophorus occidentalis*) and Great (*Podiceps major*) grebes as the goldeneyes compare with the large mergansers among the ducks. The measurements of two male and two female Hooded Grebes, respectively, are: wing (chord) 152, 162, 148, 157 mm; tarsus 46.7, 48.3, 46.6, 47.1 mm; culmen length 20.9, 22.1, —, 21.1 mm; bill from nostril 13.5, 14.5, 12.3, 13.4 mm; bill depth at posterior end of nostril 7.5, 7.6, 7.5, 7.7 mm; weight 420, 740, 530, 610 g (the last had a moderate amount of subcutaneous fat).

The head is velvety black except for the white forehead and supraorbital and postorbital areas from which narrow plumes of white, chestnut, and black extend posteriorly, the last merging with the black feathers of the crown. The forehead and crown feathers form a crest that can be raised and even held forward of the vertical. The iris is bright red, with a ring of small white spots around the pupil. Immediately behind the eye is a small, crescentic yellow wattle, unique among grebes. The neck and underparts are pure white with a black stripe (interrupted in some individuals) down the back of the neck, and a variable number of dark slaty or black feathers mixed with the white on the flanks. The back, scapulars, inner secondaries, and lesser wing coverts are black. The rest of the wing is largely white except for the inner webs of the alula feathers, the tips of the greater primary coverts, and parts of the outer primaries. The effect of these black areas is to hide the white when the wing is folded. The bill and the bare skin between the eye and the gape are dark slaty blue, as is the upper surface of the feet.

We saw no young of the species. They have been described by Nuechterlein and Johnson (1981).

Stomach Contents

Stomach contents were saved from three specimens taken by Rumboll and were analyzed by Dr. Karen Porter as follows: adult male, 16 May 1975: "Mostly well-digested and unrecognizable material. No snail shells. A few beetle larvae and fragments. Several large copepods. No insect pupae or adults. Several pebbles, a few small feathers." Adult female, 2 January 1976: "All recognizable individuals counted. Snails — 39; *Psectrocladius* sp. (Diptera, Chironomidae)—56 pupae, 1 larva; Coleoptera (Family Dytiscidae) — adults — 18 (15 of 1 species, 3 of another), larvae — 12; remainder of material appears to be well-digested snail tissue and fragments." Adult male, 8 January 1976: "Snails — much digested tissue and shell fragments. Coleoptera—one large dytiscid larva, fragments of other larvae and adults. *Psectrocladius* sp., 2 pupae. One brown flatworm?"

The stomach contents do not reflect the content of the plankton samples but indicate that Hooded Grebes take most of their food by picking items off vegetation or the bottom. This method of feeding is consistent with their rather wide bodies, short necks, and small bills.

There was no plug of feathers in the pyloric exit from the stomach, as has been the case with most grebes I have examined. Two large caecae, 7 to 8 cm long, were present. The male collected on 8 January had a large bursa of Fabricius, evidence that the bird had been hatched the preceding year. The combined weight of the pectoralis and supracoracoideus muscles of the right and left sides of the breast were 33.5 and 33.0 g, respectively.

Evidence of Breeding

Both birds collected in January were in breeding condition. The female had an enlarged oviduct, its ovary contained at least four corpora lutea, and several follicles were as much as 4.5 mm in diameter. One testis of the male measured 16 × 8 mm. Both birds had brood patches. We found no occupied nests at the time of our visit and concluded that there had been at least one unsuccessful nesting attempt before our visit.

Interactions With Other Species

The Kelp Gull (*Larus dominicanus*) is obviously feared by Hooded Grebes. When these gulls fly over, the grebes look upward at them

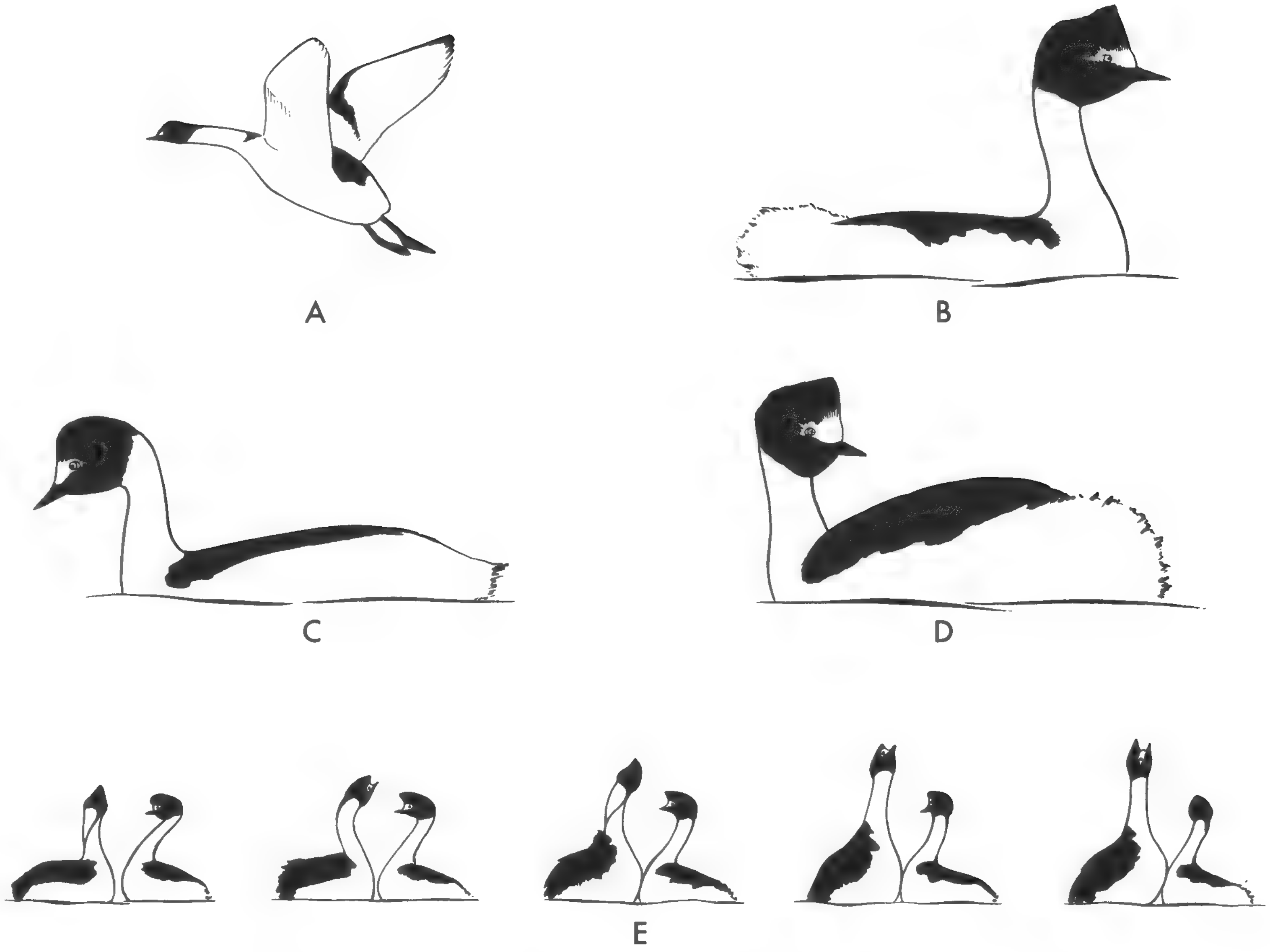


Figure 1. The Hooded Grebe. A. In flight. B. Normal swimming posture. C. Just before diving. D. Sunbathing. E. Head Flick (left bird) and Head Turning (right bird).

with their heads raised in the alert posture. If the gulls come too close, the grebes crash dive. Gulls flying overhead may set off a Penguin Dance between two grebes. In this the birds face each other and perform Head Turns and Head Flicks, and at least once, Habit Preening after the Flicks. A Penguin Dance was also seen after a grebe emerged from a crash dive. [Displays that we believed to have a signal function are capitalized; other behavioral terms are not.]

The likelihood that the Kelp Gull is a serious predator on the grebes' eggs and young was suggested to me by Maurice Rumboll; he said that the numbers of Crested Caracaras (*Polyborus plancus*) have been greatly reduced in the area by sheep ranchers and that the gulls are replacing the caracaras as scavengers. The apparent lack of nesting success could have resulted from the gulls' activities.

Locomotion

When swimming on the surface, Hooded Grebes move their feet alternately like other grebes (Figure 1B). This is particularly noticeable when the birds are pushing through beds of *Myriophyllum.* Underwater, the feet are moved synchronously. We timed 17 dives in water approximately 60 cm (about 2 ft) deep. The mean length of time spent below the surface was 21.3 sec (Standard Deviation = 2.91). Comparable figures for intervals between dives are 12.1 sec (SD = 3.50). As in other grebes, the feathers were "slicked down," which expelled air from between them and the body just before the birds submerged (Figure 1C).

The grebes made frequent upwind flights, which is not surprising in view of the strong winds on the lake. In flight, the white of the wings is very conspicuous, and a black bar extending posteriorly from the leading edge of the wing in the region of the inner secondaries divides the white into two areas (Figure 1A). On 6 January, when the wind speed varied from 65 to 80 km/hr (40 to 50 mph) and gusted to 97 km/hr (60 mph) or more, several grebes were seen flying into the wind, making slow but steady progress. From this we estimated that they can attain a flight speed of 80 km/hr or more.

Comfort Movements

We observed wing-and-leg stretches, foot-shaking, head-scratching, bathing, and various preening motions—all similar to those of other grebes. Also like other grebes, Hooded Grebes rest in the "pork-pie" posture, often with one foot tucked under the wing and flank feathers. This resting posture, named for the bird's resemblance to a pork-pie hat, appears unique among birds in that the head, facing forward, rests on the back and the bill is tucked under the side of the neck.

Sunbathing

Hooded Grebes sunbathe much as small grebes do, but the feathers of the lower back are not raised as high as are those of the smaller species (Figure 1D; cf. Storer 1969, Storer et al. 1976), possibly because of the windy environment in which Hooded Grebes live. The skin of the back and around the tail is heavily pigmented, as are the bases of the overlying feathers, much as in the Least Grebe (*Tachybaptus dominicus;* Storer et al.

1976). This pigmentation presumably absorbs solar energy while the birds are sunbathing.

Courtship Behavior

Advertising.—Although most of the birds moved about in pairs at the time of our visits, Advertising was frequent. This display was performed by single birds temporarily separated from their mates. In Advertising, the birds swam with their heads held high and their crests raised and held straight up or slightly forward (Figure 2A). The accompanying call was a rolling, high-pitched "ker-whee-eer," with the second syllable stressed and pitched higher than the other two. The call varied noticeably among individuals (Figure 3). Some sounded appreciably higher-pitched than others, possibly a sexual difference. In contrast with the Horned Grebe (*Podiceps auritus*; Storer 1969) the anterior part of the body is not puffed out, presumably because there is no color difference in this area like the contrast between the chestnut of the chest and the white of the belly in the Horned Grebe.

Bouncy Dive.—This display, used at the beginning of the Discovery Ceremony by all the "core" species of *Podiceps* except the Great Crested Grebe (*P. cristatus;* Storer 1969), was observed in similar situations in the Hooded Grebe and apparently triggered that ceremony. No Ripple Dives (as performed by the Great Crested, Silver, and Taczanowski's [*P. taczanowskii*] grebes) or Porpoising Dives (as performed by the last two species) were observed. The Bouncy Dives appeared essentially like those of the other species but were perhaps exaggerated in their stiff posture and in the more puffed-out breast. I did not see more than two Bouncy Dives in any Discovery Ceremony, but the sample size was small (4). I also did not see a diving bird go past the bird in the Cat Display, as is usual in other species that perform Discovery Ceremonies; instead they appeared to emerge in front of that bird. Here again, more observations are needed to determine whether this is always the case.

Cat Display.—This was seen three times and only as a component of the Discovery Ceremony. In each case the Cat Display (by the first bird) followed an exaggerated Bouncy Dive by the second bird, and the display was held until the second bird emerged in the Ghostly Penguin. In this Cat Display the wings were held out, almost fully stretched, and the upper surface was held forward. Because the wings are almost completely white, the display is very conspicuous. In one instance, the bird faced into the wind and in another, faced away from it. In the latter instance, the bird moved backward a third of a meter (a foot) or more as the second approached. The Cat Display of this species differs from those of the Horned and Red-necked (*P. grisegena*) grebes and resembles those of the Great Crested, Eared, Silver, and Taczanowski's grebes (Storer 1969) in that the wing is spread. The sketch I made while watching the display indicates that the wing is somewhat more spread in the Hooded Grebe than in any of the other species.

Sky Jabbing.—This display is unlike any other reported for grebes. Two birds approach each other until they meet breast-to-breast in a posture like that in a Bouncy Dive but with the bill pointed upward (Figure 4). The bill

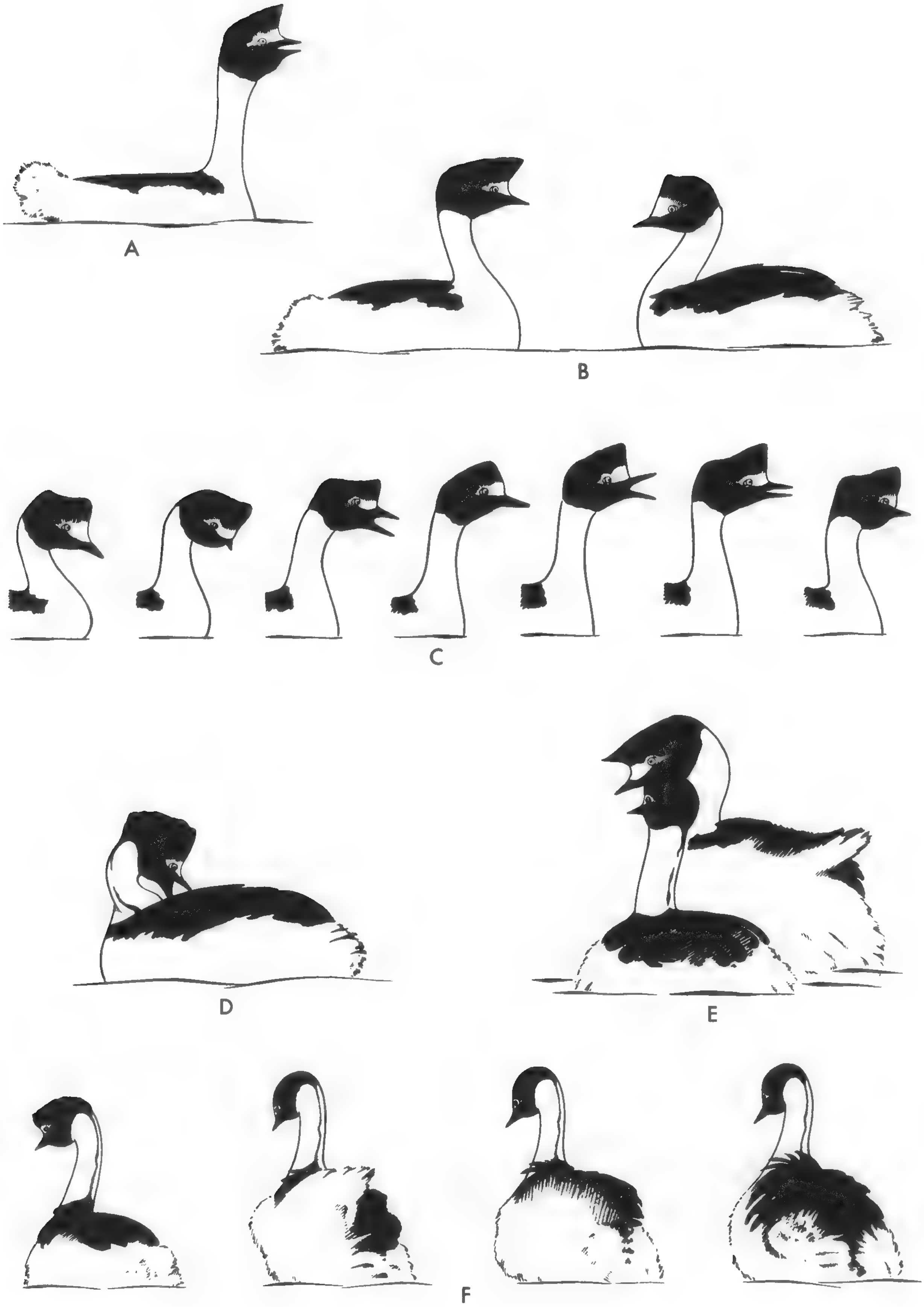


Figure 2. The Hooded Grebe. A. Advertising. B. Pair face-to-face before Penguin Dance (presumed male on left). C. Semi-flick (with double call). D. Habit Preening. E. Pair late in Penguin Dance (far bird, presumed male, Wing Quivering). F. Sequence of Wing Quivering.

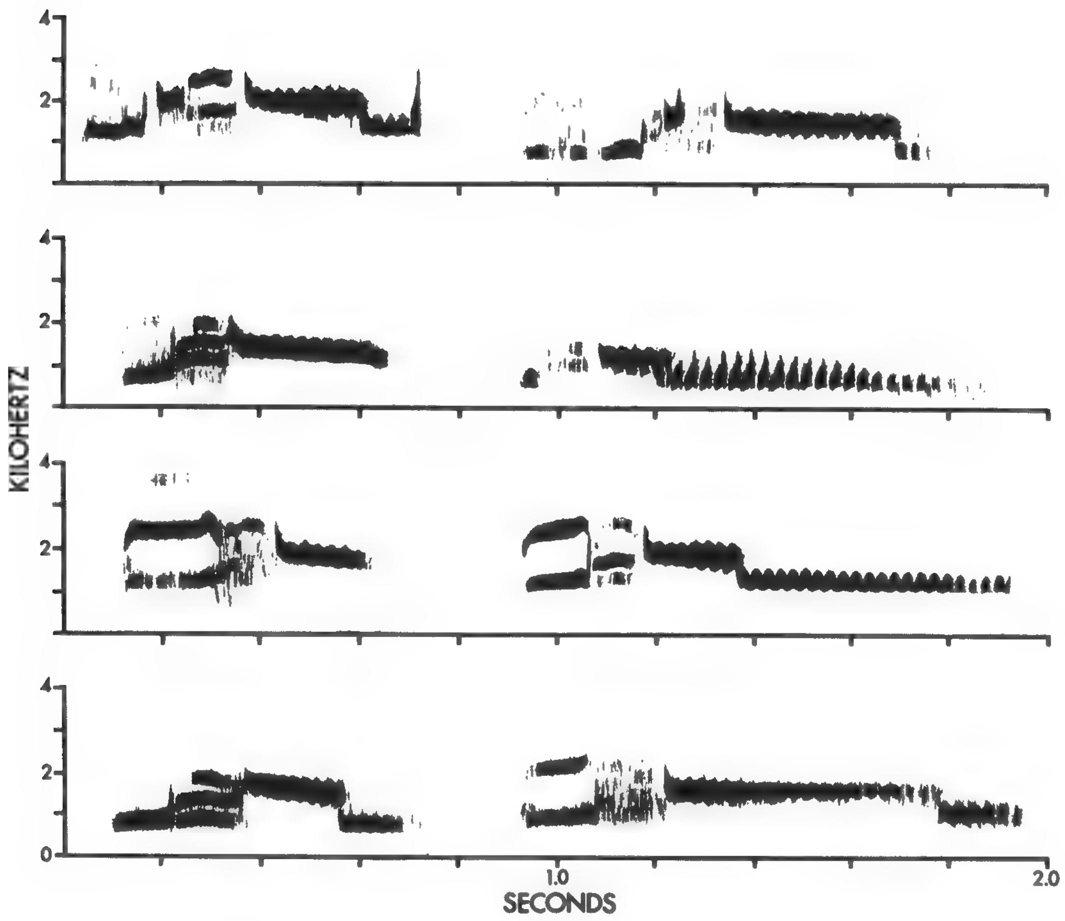


Figure 3. Hooded Grebe. Audiospectrographs of Advertising Calls of eight individuals.

is moved rapidly up and down with a motion like that of a sewing machine upside down. This display is accompanied by a call that Maurice Rumboll aptly likened to triple-tonguing on a trumpet — that is, like three notes repeated as a trill. We saw this display only twice, both times in a Discovery Ceremony between the Ghostly Penguin and Cat displays and the Penguin Dance. In the other two Discovery Ceremonies we observed, Sky Jabbing was omitted, and it may be significant that both were broken up by a third bird. We were unable to film this display. Figure 4 is based on a film made in 1980 by Gary Nuechterlein, who kindly permitted me to use it.

Head Turning. — With the bill held horizontally or pointing slightly downward, the head is rapidly turned to the right or left. The turn takes between one and three frames of cine film at 24 frames/sec and covers an arc from approximately 60° to 120° from the body axis (Figure 1E). The head is returned to the forward position, and after a short interval another turn, either in the same or the opposite direction, may be made. This was the most frequently performed display we saw and filmed, and was an important component of the Penguin Dance Ceremonies. In the latter, the birds at times alternated Head Turns and at others performed them nearly simultaneously, either moving their heads in the same direction or crossing. Head Turning is here differentiated from Head Shaking by the pauses between motions. Both are common behavior patterns in grebes and, as in the Hooded Grebe, may be performed by the same species.

Head Flicking. — The bill is pointed downward at an angle of approximately 45° and then the head is turned to the side and twisted so that one

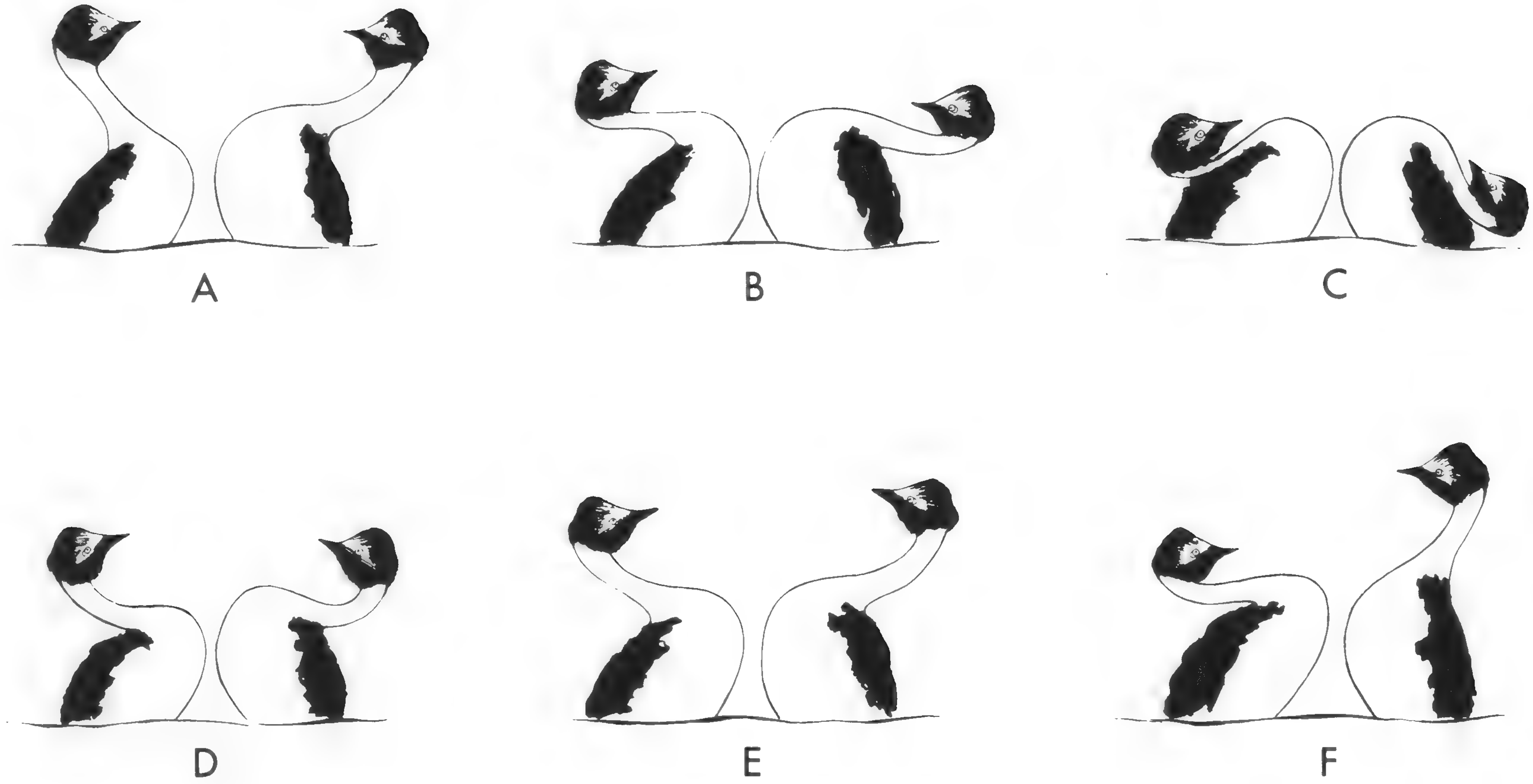


Figure 4. The Hooded Grebe Sky Jabbing Display from a cine film by Gary Nuechterlein. A—E. A sequence of synchronous movements. F. Postures during a display in which the birds' movements were asynchronous.

eye is directed upward. Next the head is flung rapidly upward so that the bill points nearly vertically (Figure 1E). The whole movement is so rapid that it was not possible to make an accurate description of it from the films. A variant of it, or perhaps a separate display, the Semi-flick, is shown in Figure 2C. In this, the movement of the head is more restricted and the bill opened at least twice. Presumably a call is given at this time, but we did not hear or record it. We saw Head Flicks performed as components of Penguin Dance Ceremonies and also in aggressive encounters between a pair and a third bird. Head Flicks were performed with Head Turns in both situations.

Habit Preening.—This consisted of turning the head to one side, reaching back, and running the beak through the scapulars (Figure 2D). It was seen as a component of the Penguin Dance Ceremony. Habit Preening in this species seems very similar to that in the Horned Grebe.

Wing Quivering.—The closed wings are raised a short distance above the body and shaken rapidly (Figures 2E and 2F). This display is a regular component of precopulatory Rearing in most, if not all, grebes. The Hooded Grebe appears to be unique in also using this display in courtship as part of the Penguin Dance Ceremonies. We also saw it performed by a bird in the prone, kink-necked soliciting posture.

Penguin Dance.—This ceremony is comparable to and homologous with the Head Shaking ceremonies of the Horned and Great Crested grebes. All are components of Discovery Ceremonies and may replace these ceremonies after the pair bond is well formed. All vary greatly in intensity. Most often, Penguin Dances are performed by Hooded Grebes facing each other (Figure 2B). They rise, breast-to-breast, with the long axis of the body at an angle of 45° or more from the horizontal, or they may remain with the body on the surface and only the necks stretched upward. The ceremony consists of a series of displays including Head Turns, Head Flicks (Figure 1E), Habit Preens, and Wing Quivering. Head Turning is the most frequent display. Usually it starts the ceremony, ends it, and is given throughout between other displays. In one sequence filmed from beginning to end, the presumed male (the bird with the longer bill and head held higher) performed 24 Head Turns (not counting 19 while approaching his mate), 4 Head Flicks, 1 Habit Preen, and 1 Wing Quivering, while the second bird performed 23 Turns, 2 Flicks, 6 Preens, and 1 Wing Quivering. In each of four filmed Penguin Dances in which all displays were performed, Head Turns appeared in the sequence first; Head Flicks (including Semi-flicks), second; Habit Preens, third; and Wing Quivering, fourth. The appearance of a display in the sequence did not preclude an earlier display from following it. As mentioned earlier, Head Turning was performed all through the ceremony, Head Flicks occasionally followed Habit Preening, and the latter once followed Wing Quivering.

Discovery Ceremony.—This complex series of displays follows a regular pattern in the grebe species that perform it. A Discovery Ceremony is usually preceded by Advertising, then as the birds approach each other, one performs a series of display dives (usually Bouncy Dives) while the other adopts the Cat Display. The last display dive ends with the diving bird rising in the Ghostly Penguin Display facing away from its partner. The diving bird then turns to face the other, and the two swim together and rise in a Penguin Dance during which a variety of displays, including Head Turning and Habit Preening, are performed. In some species like the Horned Grebe, the ceremony ends with the birds turning away from each other and swimming slowly apart with the heads held high.

We saw four Discovery Ceremonies on 30 and 31 December, but none thereafter. Unfortunately we were unable to film or tape any of them. Two ceremonies started with one bird diving toward a second and coming up in the Bouncy Posture, whereupon the second went into the Cat Display, maintaining the pose while the first made another Bouncy Dive and emerged in front of the second. Once, the emerging bird came up in what appeared to be a Ghostly Penguin attitude with its side to the bird in the Cat Display, and a Penguin Dance followed. In the other Discovery Ceremonies I did not see or did not record the posture of the emerging bird. In one ceremony, a Penguin Dance followed emergence, and in the other two, the Penguin Dance was preceded by mutual Sky Jabbing. One of the last ended with the birds turning side by side with their heads held high, as in the Ceremonial Turning Away of the Horned Grebe (Storer 1969), before resuming a normal swimming posture. The second ceremony was broken up by a third bird, whereupon the pair came back together and performed Sky Jabbing followed by a Penguin Dance.

These limited observations indicate that the Hooded Grebe performs a Discovery Ceremony like those of the "core" species of *Podiceps,* but that this ceremony may include a unique element, Sky Jabbing. What triggers the latter is not known. Emerging in the Bouncy Posture very close to a bird in the Cat Display may do this, whereas emerging in a Ghostly Penguin Display may trigger a Penguin Dance.

Platform Behavior

We saw several bouts of Weed Presentation in which the birds faced, picked up bits of *Myriophyllum,* and dropped them in front of each other. The motion was up, forward, and down, reminiscent of the head movements of New Zealand Dabchicks (*Poliocephalus rufopectus*) in their Diving Ceremony (Storer 1971). We noted no regular pattern of alternation between the members of a pair in performing this action.

The birds did not appear to be renesting; the matings we saw were on natural mats or already-made platforms of *Myriophyllum* well away from shore. The postures used in copulation are well illustrated in Erize's photographs (Conway 1980).

We did not observe precopulatory Rearing, although it may occur. Precopulatory Wing Quivering was seen once, but it was performed in the prone Inviting posture and was accompanied by a mechanical side-to-side turning of the head. Before mounting, the active bird adopted an "oblique-necked advertising" posture like that of the Horned Grebe (Fjeldså 1973). After copulation, the birds faced and performed Head Shaking with the heads held high.

Comparisons With Other Species

The Hooded Grebe shares the complex Discovery Ceremony with the other "core" species of *Podiceps* (the Horned, Red-necked, Great Crested, Eared, Silver, and Taczanowski's grebes). This ceremony in the

Hooded Grebe is unique in two respects — the interpolation of a Sky Jabbing Display, and the use of Wing Quivering in the Penguin Dance. Because the Hooded Grebe includes more than one display, its Penguin Dance Ceremony differs from those of the Horned, Red-necked, and Eared grebes, and the homologous Head Shaking Ceremony of the Great Crested Grebe. Silver and Taczanowski's grebes also have more than one display in the Penguin Dance Ceremony. In lacking a Weed Ceremony, the Hooded Grebe differs from the Horned, Great Crested, and Red-necked grebes and resembles the Eared, Silver, and Taczanowski's grebes. The four Northern Hemisphere species (Horned, Red-necked, Great Crested, and Eared grebes) are sympatric in various combinations. All have Discovery Ceremonies that vary little within species. For example, Great Crested Grebes regularly perform Ripple Dives before the Ghostly Penguin Display, whereas the other three use Bouncy Dives in this situation. The climax of the Discovery Ceremony, a Penguin Dance in all except the Great Crested, is accompanied by a single display (e.g. Head Shaking in the Great Crested and Habit Preening in the Horned). In contrast, the South American species (Silver, Taczanowski's, and Hooded grebes) are more variable in their Discovery Ceremonies.

The Discovery Ceremony appears to function in pair formation and in strengthening the pair bond. Hence selection would presumably act to establish and maintain signals by which an individual grebe could recognize another bird of its own species, thus reducing the likelihood of losing its reproductive potential through mating with another species. Clues that may function in this way include differences in the call that precedes the Discovery Ceremony, in the plumage (especially the head), and in the Discovery Ceremony. With one exception, the first two differences are found in all species of *Podiceps*. As is evident from the foregoing discussion, Northern Hemisphere *Podiceps* have interspecific differences in such Discovery Ceremony elements as the approach dives, Cat Display, and the climax of the ceremony, but each species shows little or no *intraspecific* variation in these elements. In contrast, the South American Silver and Hooded grebes have considerable intraspecific variation in some of these elements, and at least one interspecific difference — the Hooded Grebe's interposition of the unique Sky Jabbing Display between the Ghostly Penguin and the Penguin Dance. The Discovery Ceremony of the Hooded Grebe is also unique in the inclusion of Wing Quivering in the Penguin Dance, a display heretofore known in grebes only in precopulatory soliciting. (Taczanowski's Grebe, a very recent offshoot of the northern form of the Silver Grebe, is not included in this discussion because I was unable to note any differences between its behavior and that of the Silver Grebe. The Great Grebe has such a completely different set of courtship displays that it might be considered generically different.)

The known breeding range of the Hooded Grebe lies wholly within that of its widespread Temperate Zone relative, the Silver Grebe. Whether the two evolved in sympatry or allopatry is unknown, but probably the range of the Hooded Grebe was once more extensive than it is now. The rising of the Andes has gradually increased the rain shadow effect on the areas to the east. While flying over part of this region, I noted that many of the small lakes seem to be in the process of becoming increasingly full of salts and drying up.

THE SEARCH FOR OTHER POPULATIONS

On 17 January we took off from Calafate in a chartered 4-passenger plane and flew the route shown in Figure 5. (For localities mentioned in this account, see the map for Zone 8 published by the Automóvil Club Argentino.) We crossed the north shore of Lago Argentino just west of Estancia La Angostura and proceeded almost due north to Lago Viedma. On the intervening plateau we saw seven lakes, two near the south edge of the plateau, four in a group somewhat farther north, and a single one a short distance south of the valley of the Río Guanaco. One lake of each of the first two groups appeared to contain *Myriophyllum,* but both lakes were drying up. The single lake near the Río Guanaco appeared dark blue with patches of *Myriophyllum,* and we could see flamingos and swans on it, but could not identify smaller birds. We crossed over the north shore of Lago Viedma east of Ea. Viedma and found not one, but a series of six lakes between Highway 524 and the lake. There appeared to be no *Myriophyllum* on them, nor obvious large birds. "Laguna La Rubia" shown on the map proved to be a complex of ten lakes, with another six visible off to the east. The two largest of the La Rubia complex were yellow or yellowish brown and as far as we could see were without birds, but three of the smaller lakes appeared blue-black, contained *Myriophyllum,* and had birds on them. Thence we flew south over Ea. La Meseta, which had a complex of lakes east of the Río La Leona. This consisted of a larger lake just to the north of the escarpment forming the northern edge of the valley of the Río Santa Cruz, and a group of four smaller lakes on the slopes of the escarpment. The large lake and one of the four smaller ones were blue-black and contained *Myriophyllum.* From here we could see seven more lakes to the

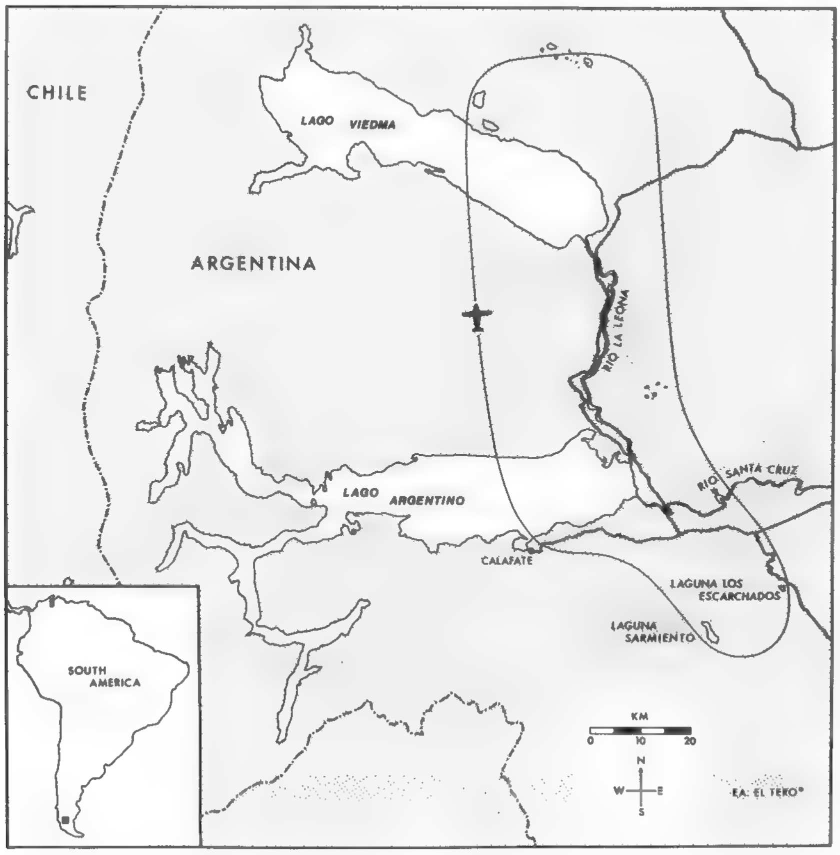


Figure 5. Map of flight taken in search of suitable habitat for the Hooded Grebe.

east. We then flew south over the valley of the Río Santa Cruz to Los Escarchados which proved to be a complex of three lakes — Los Escarchados itself, a smaller lake (Escarchados Chico) to the west, and another small lake north of Highway 40 and slightly east of the large lake. Neither of the two small lakes is visible from the road; both appeared blue-black and contained *Myriophyllum.* We then turned northwest and flew over Laguna Sarmiento, which appeared white, possibly saline, and had approximately 20 flamingos in its northwest corner. A smaller lake to the southeast of it appeared brownish but had birds on it. Between Laguna Sarmiento and the rim of the plateau at the Rio Bote were two more small lakes, one blue-black and one nearly white. Between the Río Bote and Calafate we saw four more small lakes, three white and one dry. We landed at Calafate at 10:45 AM.

These lakes in the rain shadow of the Andes must depend on snow melt for their water and appear to be drying up. The below-normal snowfall the previous winter presumably was responsible for the low levels of many of the lakes we flew over. Nevertheless we saw several that appeared suitable for the Hooded Grebe: the lake south of the Rio Guanaco, three small lakes in the La Rubia complex, at least the large lake at La Meseta, the two small lakes near Los Escarchados, and possibly one of the small lakes north of Laguna Sarmiento.

On 18 January I went on foot to the Laguna de Los Escarchados Chico. As in the larger lake, the water was low, but there were several hundred ducks, mostly Chiloe Wigeons, 46 Black-necked Swans, 1 Coscoroba Swan, 2 Chilean Flamingos, and a single White-tufted Grebe. In years of higher water this lake might be suitable for Hooded Grebes, but at the time of my visit there was little water between the central mat of *Myriophyllum* and the shore.

On 15 January we visited Ea. El Tero in the Arroyo del Italiano at the invitation of the owner, Mr. Clark, and checked the two lakes near the house. These lakes were connected to the stream in the arroyo, contained clear water and beds of *Myriophyllum,* and were stocked with trout. In them we found a dozen or more White-tufted Grebes, but no Hooded Grebes, and were told by the manager, who knows *Rollandia* well, that he had never seen any birds resembling Hooded Grebes there.

We made two unsuccessful trips west from Calafate looking for Great Grebes and other colonies of Hooded Grebes. On 3 January we drove to Punta Bandera, where there are three ponds containing waterfowl, and then around .the north shore of Brazo Rico to the Glaciar Moreno; on 5 January we visited Lago Roca.

On 7 January Pierre and Jean Devillers flew from Calafate to Río Gallegos, noting the lakes that they could see en route. At least six of these seemed to contain *Myriophyllum,* but the water appeared white, not dark blue.

In our limited search for lakes suitable for Hooded Grebe nesting, we found as many as eight in the area we covered, and there probably are a good many more elsewhere. We flew over only a small portion of the potentially suitable country and did not investigate the lakes in the more mesic region nearer the Andes. Aerial surveys, preferably by helicopter, are clearly needed to determine the breeding range of the Hooded Grebe.

POPULATION SIZE AND DISTRIBUTION

We found Hooded Grebes only on Los Escarchados. On four occasions I walked around that lake and counted the grebes, finding 126, 116, 52, and 63 on 28 December and 6, 13, and 18 January, respectively. The count on 13 January was probably low, but it was clear that by this date approximately half of the birds had departed. The most Silver Grebes I counted was 37 on 6 January. In 1978 Erize (MS) found Hooded Grebes on two other nearby lakes, on one of which they bred. The number of potentially suitable lakes seen from the air in the small area surveyed suggests that there may be other, as yet undiscovered, populations of the species.

The wintering grounds have not been found. In preparing specimens we found well-developed salt glands over the eyes, indication that the birds spend part of the year (presumably the winter) on salt water. Los Escarchados is nearly equidistant from the deep, sheltered Chilean fjords and the lee coast of Argentina. The wide body, short neck, and small bill of the Hooded Grebe indicate that these birds are adapted for feeding on slow-moving, probably benthic, organisms, and this is borne out by their diet on the breeding grounds. Thus the birds probably winter on the estuaries or near the shore on the Argentine coast, rather than on the deeper Chilean fjords, which would have to be reached by flying over the Andes. After the wintering grounds are found and censused, we will have a better idea of the total population size.

CONSERVATION

Until a better estimate of the total population can be made, conservation measures must be based on the most pessimistic view: that the birds on Los Escarchados form the bulk of the population. These measures should include protecting the habitat, guarding the birds from human interference, controlling the Kelp Gull, investigating factors affecting reproductive success, and searching for other breeding populations and the species' wintering grounds. The Fundación Vida Silvestre Argentina, under the direction of Francisco Erize, has already made great strides in this important conservation effort.

SUMMARY

Hooded Grebes are wide-bodied, short-necked, and short-billed; they feed on invertebrates such as snails, leeches, water beetles, and midges. They are known only from Laguna de Los Escarchados and two nearby lakes in southern Patagonia, Argentina. A brief aerial survey resulted in finding several other lakes in the region potentially suitable for the species' breeding. Their wintering grounds are unknown, but presumably are on salt water.

Hooded Grebe behavior is generally similar to that of other species of *Podiceps*, but differs in at least two respects: A unique Sky Jabbing display is at times included in the Discovery Ceremony; and Wing Quivering, used by other grebes only as a precopulatory display, is also used by Hooded Grebes in the Penguin Dance, a courtship display.

Acknowledgments

Of the many people who helped with this study, I am particularly grateful to Maurice A. E. Rumboll, who made the necessary arrangements; to Miguel Hinrichsen, who provided the transportation; and to James Hammond, who was responsible for the photography and sound recordings. All three provided congenial company and assisted in many ways. Dr. Karen Porter identified invertebrates in the plankton samples and stomach contents; Dr. John B. Burch, the mollusks; and Dr. Rogers McVaugh, the plants. Drs. John T. Lehman and Peter Kilham gave advice on limnological matters, Don Ernesto Lenzner arranged for the aerial survey, and Mark Orsen and Margaret Van Bolt prepared the illustrations. The work was generously supported by a grant from the National Geographic Society.

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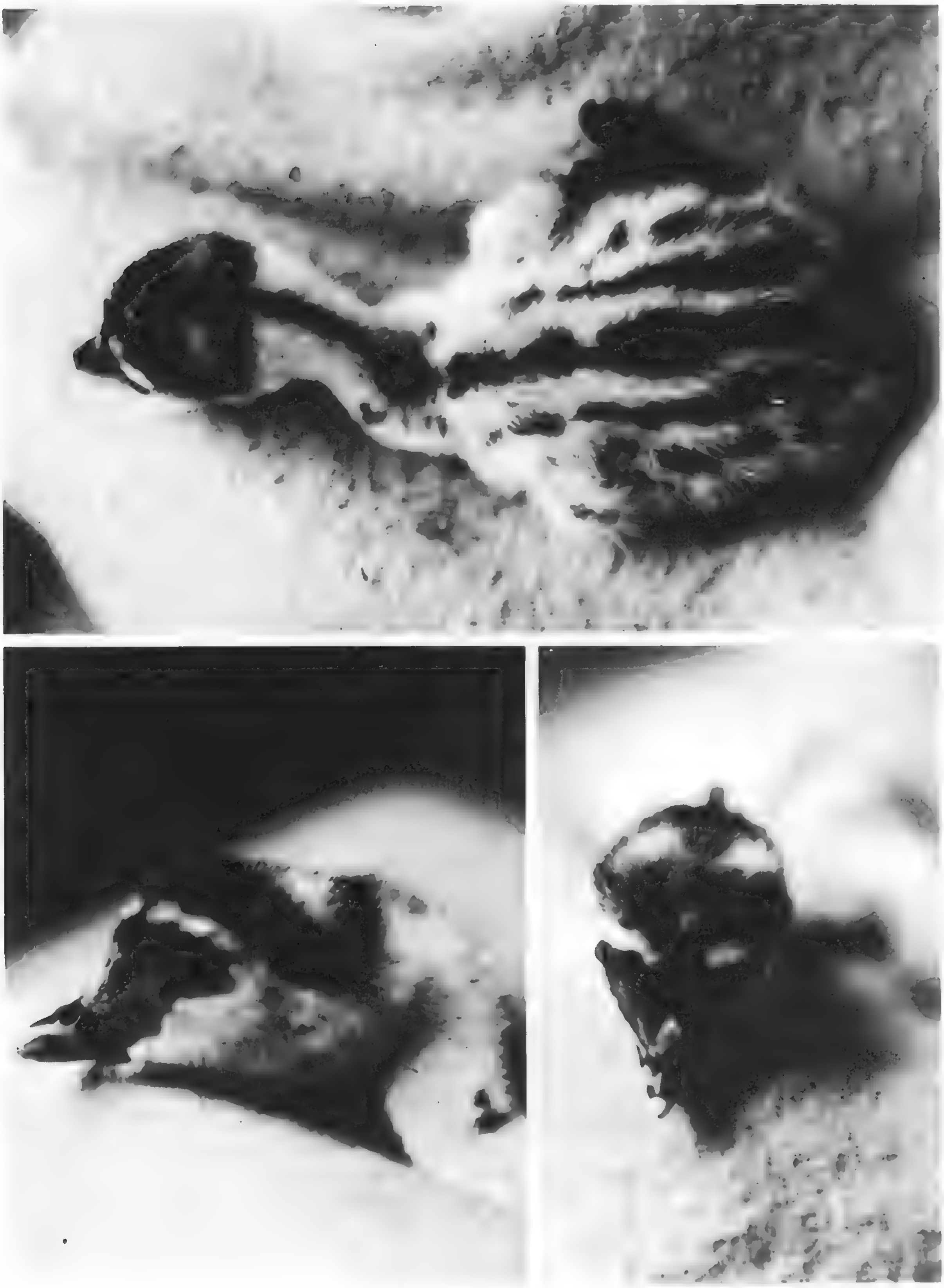

Figure 1. One-day-old Hooded Grebe chick. Dorsal view of back (top); lateral and dorsal views of head (bottom).

THE DOWNY YOUNG OF THE HOODED GREBE

GARY L. NUECHTERLEIN AND ANDRES JOHNSON

Rumboll's recent (1974) description of a striking new species of grebe in southern Patagonia, Argentina, has aroused considerable interest among both avian systematists and conservationists (Storer 1981, Erize in press). Since its discovery and Storer's initial studies, the Hooded Grebe (*Podiceps gallardoi*) population at the Los Escarchados reserve near Calafate, Santa Cruz, Argentina, has experienced repeated reproductive failures; fewer than 15 young are known to have fledged successfully. Counts of adults have dwindled from an estimated 126 birds in 1976 (Storer 1981) to fewer than 80 individuals in 1980–81. In the 1979–80 and 1980–81 breeding seasons birds dispersed and attempted nesting on several smaller, at times inaccessible, lagoons of the area. Because this is the only known population, the species appears to be in trouble.

From December 1980 to February 1981, we camped on the shores of one of these small remote lakes, named Blanquillo, and began a study of the selective pressures acting on the Hooded Grebe. We also initiated several effective measures against predators and competitors, and all 14 pairs with nests on the lake successfully hatched young. During these studies the birds became extremely tame, which gave us an opportunity to photograph and observe closely the previously undescribed downy young of this species. Knowledge of the patterns of newly hatched downy grebes is of major importance phylogenetically (Storer 1967), and we here present a brief description and illustrations of the chicks.

NESTING BIOLOGY

On Lake Blanquillo each of the 14 Hooded Grebe nests contained only two eggs. This is the smallest mean clutch size reported for any species of grebe. The clutch size ranges from 2–4 eggs for Western Grebes (*Aechmophorus occidentalis*) to 4–7 for Pied-billed Grebes (*Podilymbus podiceps*). As in other grebes the eggs hatch asynchronously, but in this case all pairs abandoned the second egg of the clutch soon after the first had hatched. The abandoned eggs of the first nests were immediately preyed upon by Red-gartered Coots (*Fulica armillata*) and Kelp Gulls (*Larus dominicanus*). This prompted us to salvage eggs left in later nests. We attempted to incubate two of these eggs, from which one chick hatched but died 4 days later.

Hatching of the Chick

In the egg we incubated successfully, the chick began peeping from inside the intact egg the day before hatching. On the morning it hatched, we regularly checked the egg in anticipation of actually seeing the chick emerge. The hatching process was extremely rapid, less than 20 minutes from first pipping to complete emergence from the egg. This observation was confirmed by data from natural nests and agrees with the rapid hatching rates recorded in other grebes (G. Nuechterlein, R. W. Storer, pers. obs.). Presumably, accelerated hatching may relate to the danger of being directly exposed to, or trodden into, the sodden nesting material while beneath the parents. In the nesting colony a newly-hatched chick usually climbed onto the back of the incubating parent within 5–10 minutes of emergence, which behavior might also relate to the wetness of the nest.

THE DOWNY YOUNG

The striped Hooded Grebe chick (Figure 1) most closely resembles that of the Silvery Grebe (*Podiceps occipitalis;* Storer 1967). The back is boldly streaked with seven longitudinal black stripes, separated by white stripes of similar breadth. As in other *Podiceps,* the dark mid-dorsal stripe is uninterrupted over the back; the three lateral dark stripes on either side are broken into blotches, with the ventralmost the most interrupted. Only the dark mid-dorsal stripe extends anteriorly up the neck to the head. The first dark lateral stripe on either side continues past the base of the neck but is broken into blotches reaching halfway up the neck. All ventral parts are unstreaked and white, except for a dark, unconnected medial stripe on the neck.

The feet and tarsi are dark gray. The bill is mostly black above and light below, with a diagonal dark stripe extending downward toward its base; the eggtooth is white. The head is mostly black dorsally except for white "eyebrows" and a patch of diffuse white down on the posterior sides of the crown. In this respect the Hooded Grebe chick resembles the Silvery Grebe chick.

There is one important exception. Unlike any other *Podiceps* or even the related Western Grebe, the Hooded Grebe chick has *no* bare patch of skin on the forecrown. This skin contains instead a small triangular-shaped patch of white down. There is, however, a well-developed bare skin area immediately posterior to the bill in the loral region.

DISCUSSION

The downy patterns of the Hooded Grebe largely support morphological and behavioral evidence (Rumboll 1974, Storer 1981) that the species is placed correctly in the genus *Podiceps.* The chick is aberrant only in lacking a bare crown patch. The functions of head patches of grebes are poorly understood, and the significance of this trait is therefore difficult to assess. In at least the Eared Grebe (*Podiceps nigricollis*) and Western Grebe, the crown patch can flush rapidly from a pale yellow to a deep crimson (Storer 1967), particularly when the chick is hungry or in distress (Nuechterlein pers. obs.). Possibly this attracts parents to the particular member of their brood that is peeping and in need of attention. It also may be that within the single-chick broods of Hooded Grebes, this "signaling" is superfluous. Also, the well-developed bare loral patch of Hooded Grebe chicks appears capable of changing color from pale yellow to crimson. Such loral patches are nearly universal among grebes (Storer 1967), but vary widely in size and presumably in degree of vascular development. If appropriate techniques are used, grebe chicks are easily managed as experimental subjects (Nuechterlein 1981), and this area of research certainly merits further investigation.

Acknowledgments

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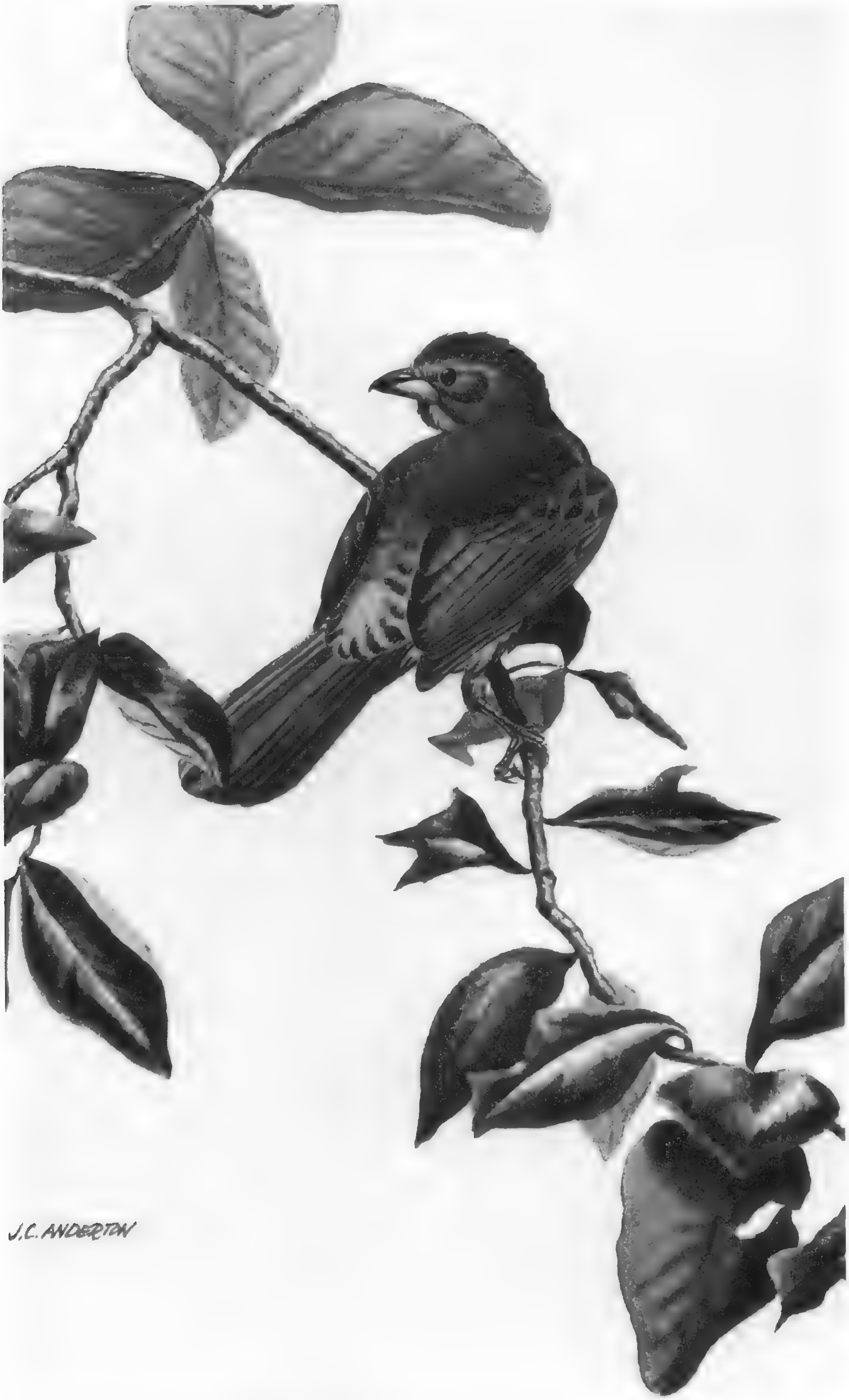
JAMES FORD BELL MUSEUM OF NATURAL HISTORY
UNIVERSITY OF MINNESOTA
10 CHURCH STREET S.E.
MINNEAPOLIS, MINNESOTA 55455

Present address:

MUSEUM OF ZOOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN 48109

and

FUNDACIÓN VIDA SILVESTRE ARGENTINA
MAIPU' 471, PISO 11
1006 BUENOS AIRES, ARGENTINA



Silver-beaked Tanager, *Ramphocelus carbo.* Sepia wash drawing of female from field sketch made in Trinidad by John C. Anderton.

RELATIONSHIPS AND SPECIATION OF THE HAWAIIAN THRUSHES

H. Douglas Pratt

The Hawaiian Islands, separated from the nearest land masses by more than 4,000 km (2,500 mi) of open ocean, are among the most isolated islands in the world and are of relatively recent volcanic origin (Pliocene age for all main islands except Hawaii, which is Pleistocene). Their modern native land birds are believed to have evolved from only a few original colonizing species: one or two rails, a goose, a hawk, an owl, a crow, two honeyeaters, a small flycatcher, a warbler, a siskin-like finch, and a thrush (Mayr 1943). These colonizers are thought to have spread through the archipelago and adapted differentially to the environment of each island. When a new species formed, it could then reinvade a parent island. By such speciation and recolonization, a bird community of remarkable diversity evolved. Indeed, the Hawaiian honeycreepers (Drepanidinae), an endemic subfamily (Pratt 1979) related to cardueline finches (Raikow 1976), are among the most impressive avian examples of adaptive radiation. Much less spectacular than the oft-cited honeycreepers are the rather plain brown and gray native thrushes. Traditionally classified as an endemic genus, *Phaeornis,* the Hawaiian thrushes have not differentiated nearly as much as have the honeycreepers. They therefore provide an excellent opportunity to study adaptive radiation in its earliest stages.

MATERIALS AND METHODS

This study was part of a broad investigation of Hawaiian birds (Pratt 1979) that involved both specimen analysis and field observation. I originally gathered data on the thrushes to determine how many species should be recognized, and later extended the study to include the mainland (continental) ancestry of the group. The following discussions combine my own observations with the sparse literature on the appearance and natural history of the thrushes. The reader should understand that published data are limited but may represent all that will ever be known about some of these birds—most of them are rare or extinct (Berger 1981). My discussions of the Hawaiian birds' relationships to mainland thrushes are based on the literature and on my studies of museum skins and taped vocalizations.

I examined specimens at the Bernice P. Bishop Museum (BBM), American Museum of Natural History (AMNH), Louisiana State University Museum of Zoology (LSUMZ), and the Library of Natural Sounds (LNS), Cornell University. I conducted field work in Hawaii intermittently from 1974 to 1979. Most of my observations took place on the island of Hawaii, but from 28 June to 8 July 1975 I investigated the two thrush species in the Alakai Swamp on Kauai. I also participated in a successful search for the thrush of Molokai, 20–25 July 1975 (Scott et al. 1977), but did not personally see the bird. In the early part of the study I concentrated on collecting sound recordings of songs and call notes later used in playback experiments. I studied my own recordings, those made by Gauthey et al. (1968) on Kauai, and archived LNS sound specimens. All of these recordings are now in the LNS collection.

The Kamao (*Myadestes myadestinus*) of Kauai in lapalapa (*Cheirodendron kauaiense*), a favorite food source. Painting by H. Douglas Pratt.

THE HAWAIIAN THRUSHES: AN OVERVIEW

Six forms of *Phaeornis* from five different islands have been described, originally as separate species—*obscura* (Gmelin) 1789 of Hawaii; *lanaiensis* Wilson 1891 of Lanai; *rutha* Bryan 1908 of Molokai; *oahensis* Wilson and Evans 1899 of Oahu; and *myadestina* Stejneger 1887 and *palmeri* Rothschild 1893, both of Kauai. Figure 1 shows the distribution of these forms with their Hawaiian vernacular names. Since the Hawaiian names are taxonomically noncommittal, I shall make frequent use of them in the following discussions:

The Amaui (on Oahu) became extinct shortly after its discovery in 1826, and no specimens of it are known; the name *oahensis* was based on written descriptions only (Wilson and Evans 1890–99). The Hawaiians did not differentiate between the thrushes of Molokai and Lanai and used the name Olomao for both. Although never seen by ornithologists, a thrush probably also existed on Maui (Munro 1960). Kauai is the only island known to have more than one thrush species. For many years the smaller Puaiohi, *P. palmeri,* has been considered a monotypic species while the larger Kamao, *myadestina,* has been "lumped" with all the other forms under the name Hawaiian Thrush, *P. obscura.* Thus only two species are currently recognized in the genus, with the larger one having a different subspecies on each of the islands it inhabits.

Hawaiian thrushes are solitary, highly sedentary birds that live primarily in dense montane forests. On Kauai, both species are now confined to the Alakai Swamp, a boggy cloud-forested plateau in the central highlands. The Puaiohi has always been considered rare (Perkins 1903), but the Kamao was common until relatively recent times (Munro 1960). The Olomao was common in the small rainforest tract on Lanai until the 1920's, but then declined rapidly and is now believed to be extinct (Munro 1960). It barely holds on in a remnant of the original rainforest of eastern Molokai (Scott et al. 1977). In contrast, the Omao of Hawaii maintains a fairly high population and could even be considered locally abundant, especially in the rainforests of the windward Hamakua Coast and areas north and east of Hawaii Volcanoes National Park. It has, however, disappeared from some places where it formerly lived, such as the upper rainforests of the leeward Kona Coast (van Riper and Scott 1979). The Omao also occupies a wider range of habitats than do the other Hawaiian thrushes. I have found Omao often in scrubby ohia-lehua (*Metrosideros collina*) trees growing on relatively recent lava flows in the central "saddle" of the island. An isolated population of Omao lives also above tree line on Mauna Loa among low shrubs; the birds perch on rocks rather than trees (Dunmire 1961).

All Hawaiian thrushes eat small fruits, such as those of olapa (*Cheirodendron* spp.), but the birds also take insects, often by flycatching (hawking). The Puaiohi is primarily insectivorous (Perkins 1903). All the larger forms forage primarily in the forest canopy and only rarely go to the ground. The Puaiohi has most often been seen in the understory near, but not on, the ground. The many published illustrations that show Hawaiian thrushes on the ground are misleading and may partly account for the reluctance of some ornithologists to accept the idea that these island birds are closely related to the highly arboreal New World solitaires of the genus *Myadestes.*

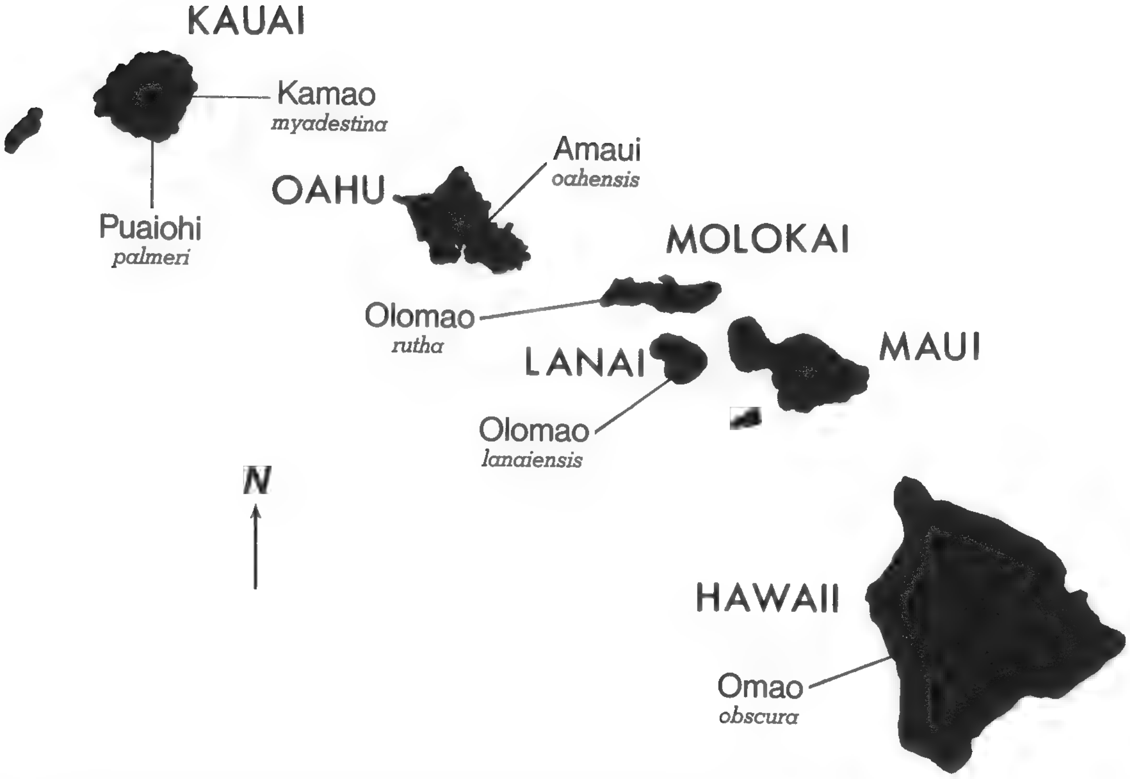


Figure 1. The Hawaiian Islands showing the distributions and native names of the six known forms of Hawaiian thrushes. Pronunciation of native names is as follows: consonants as in English; *a* as in father, *i* as in machine, *o* as in home, *u* as in lute, *ai* as eye, *ao* as *ow* in fowl, *au* as in Faust.

RELATIONSHIPS

The striking similarity of the Hawaiian thrushes to American solitaires were first noted by Stejneger (1887) in his description of *Phaeornis myadestina.* Later, Stejneger analyzed the relationships of *Phaeornis* and *Myadestes* in more detail. In comparing the Kamao with Townsend's Solitaire (*M. townsendi*), Stejneger (1889: 383) stated that "were it not for the different proportions of wing, tail, and legs, the two birds could hardly be separated generically." Other authors (Amadon 1942, Ripley 1952, Ames 1975) supported a close relationship of *Phaeornis* to *Myadestes,* but E. H. Bryan (1940) inexplicably associated *Phaeornis* with several Old World genera far removed from the American solitaires. Ripley (1962) later changed his opinion after hearing and seeing *Phaeornis* (probably only *obscura*) in the field. He thought that vocal behavior of the Hawaiian birds showed a close relationship with the nightingale-thrushes of the genus *Catharus.* Ripley (1964) placed *Phaeornis* next to *Catharus* in "Peters' Check-list."

The genus *Myadestes* comprises seven or nine species (depending on whose taxonomy one follows). All except Townsend's Solitaire are sedentary tropical birds. The genus is distributed from central Alaska south through Mexico, Central America, the West Indies, and the Andes of South America. Solitaires are usually considered to be aberrant thrushes, although Sibley's (1973) study of egg white proteins and Ames's (1975) work on syringeal morphology suggested that solitaires might be related to some other passerine group. More recently, Sibley and Ahlquist (in press) have evidence from DNA hybridization studies that shows solitaires to be thrushes after all.

The genus *Catharus* comprises 11 species that can be divided into two groups, the first of which contains four species—the Hermit (*C. guttatus*), Swainson's (*C. ustulatus*), and Gray-cheeked (*C. minimus*) thrushes, and the Veery (*C. fuscescens*)—that breed in temperate North America and migrate to the tropics (Dilger 1956). The second is a group of sedentary neotropical birds known as nightingale-thrushes, and it is to this subgroup that Ripley (1962) considered the Hawaiian thrushes related. Nightingale-thrushes are found throughout the Neotropics except for the West Indies and Amazonia. Members of this genus are typical thrushes in every respect.

The following comparisons are made to test Ripley's hypothesized close relationship between *Catharus* and *Phaeornis,* in contrast to Stejneger's assertion that *Phaeornis* and *Myadestes* can hardly be generically separated.

APPEARANCE

Coloration

Phaeornis and *Myadestes* are strikingly similar in plumage coloration. Adult solitaires are clad in somber tones of gray and brown, the brown tones usually being confined to the upper surface. A few species have white eye-rings and some have dark malar streaks. All but the Rufous-brown Solitaire (*M. leucogenys*) have the outer tail feathers tipped with white. In some species the white extends up the outer webs of the outer rectrices, giving the folded tail a white border, whereas in others the outer webs are paler than the inner ones, but are not white. The primaries are marked by a pale band at their base, and their outer webs form a pale rectangular patch on the folded wing. Only the Rufous-throated Solitaire (*M. genibarbis*) of the West Indies exhibits any striking patterns or color contrasts.

Immature *Myadestes,* very different from the adults, are dark and heavily "spotted" above and below in a manner unusual among thrushes. The feathers of the breast are pale in the center but have a dark border, and thus might better be called "scalloped" rather than spotted. Among New World thrushes, only the solitaires and bluebirds (*Sialia*) have such scalloping. Dorsal feathers of immature solitaires are brown or gray basally, with a darker border and a subterminal buffy spot. Species of solitaires differ subtly in hue, but vary only slightly from the pattern described.

A general description of the coloration of Hawaiian thrushes would repeat the foregoing almost verbatim, except that they are even more alike than are the solitaires. Color contrasts are less striking in the Hawaiian birds, but all have more-or-less white tips and pale outer webs to the tail feathers, and all have a pale wing patch exactly like that of solitaires. Adults never have spotted undersides, and the immature thrushes are dark brown and scalloped in precisely the same manner as are young solitaires. So similar are the Hawaiian thrushes to the solitaires that both adult and immature specimens of the thrushes can be easily "lost" in a tray of solitaire study skins (Figure 2). If the Hawaiian thrushes were placed in the genus *Myadestes,* their somewhat duller and less-contrasting plumage could be an illustration of trends noted elsewhere in island representatives of mainland genera (Grant 1965b), although the Rufous-throated, the most brightly plumaged solitaire, is a island dweller.

The plumage of the *Catharus* thrushes is also generally dull. Nightingale-thrushes often have red or orange bills, legs, and eyelids. Brightly colored bills also occur in some solitaires—the Andean (*Myadestes ralloides*), Black-faced (*M. melanops*), and Varied (*M. coloratus*)—but no solitaire has a brightly colored, fleshy eye-ring. Since bright eye-rings are generally common among thrushes, the lack of eye-rings in solitaires and Hawaiian thrushes may be noteworthy. All temperate region *Catharus* and some nightingale-thrushes have ventral spots in the adult plumage, and immature birds are heavily spotted (not scalloped) above and below. No *Catharus* shows any white in the tail or a pale patch at the base of the primaries on the closed wing.

Postures

Hawaiian thrushes characteristically perch upright, with the tail pointing downward and the wings often slightly drooped (Figure 3). I have never seen Hawaiian thrushes perch on the ground, although they apparently do so occasionally (Perkins 1903, Dunmire 1961). Solitaires also have an upright posture, unusual for thrushes. Their somewhat flycatcher-like stance is shown in well-executed illustrations such as those in Peterson and Chalif (1973), Bond (1974), and Ridgely (1976). *Catharus* thrushes perch in the somewhat horizontal posture characteristic of many thrushes. They often perch on the ground, and hop in the familiar manner of the American Robin (*Turdus migratorius*) (Bent 1949, Slud 1964).

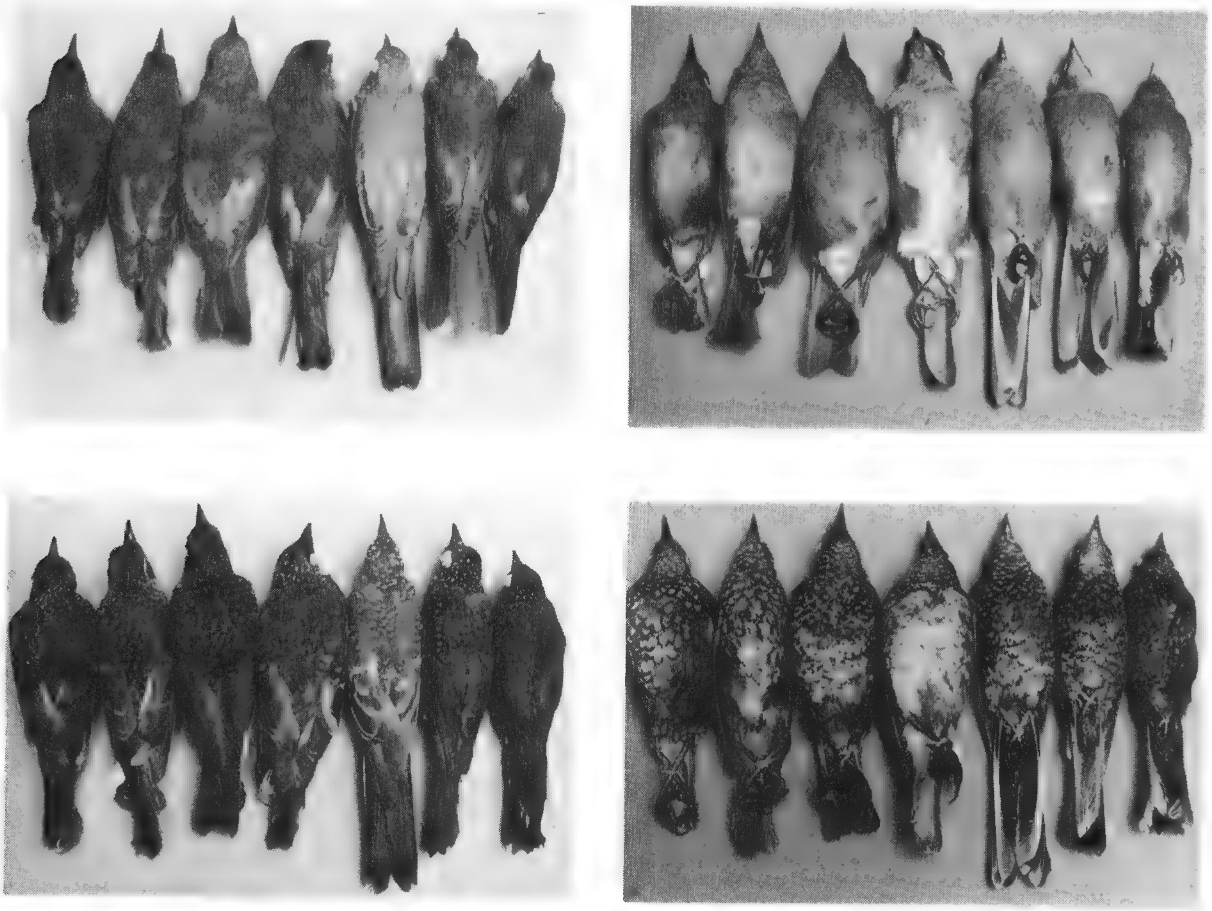


Figure 2. Study skins of Hawaiian thrushes and selected solitaires. Upper row, adults; lower row, immatures. Left, dorsal aspect; right, ventral aspect. Species, left to right in each photograph: *Myadestes* (*"Phaeornis"*) *palmeri*, *M. lanaiensis*, *M. obscurus*, *M. myadestinus* (all Hawaiian); *M. townsendi*, *M. occidentalis* (formerly *obscurus*), *M. ralloides* (all mainland species).

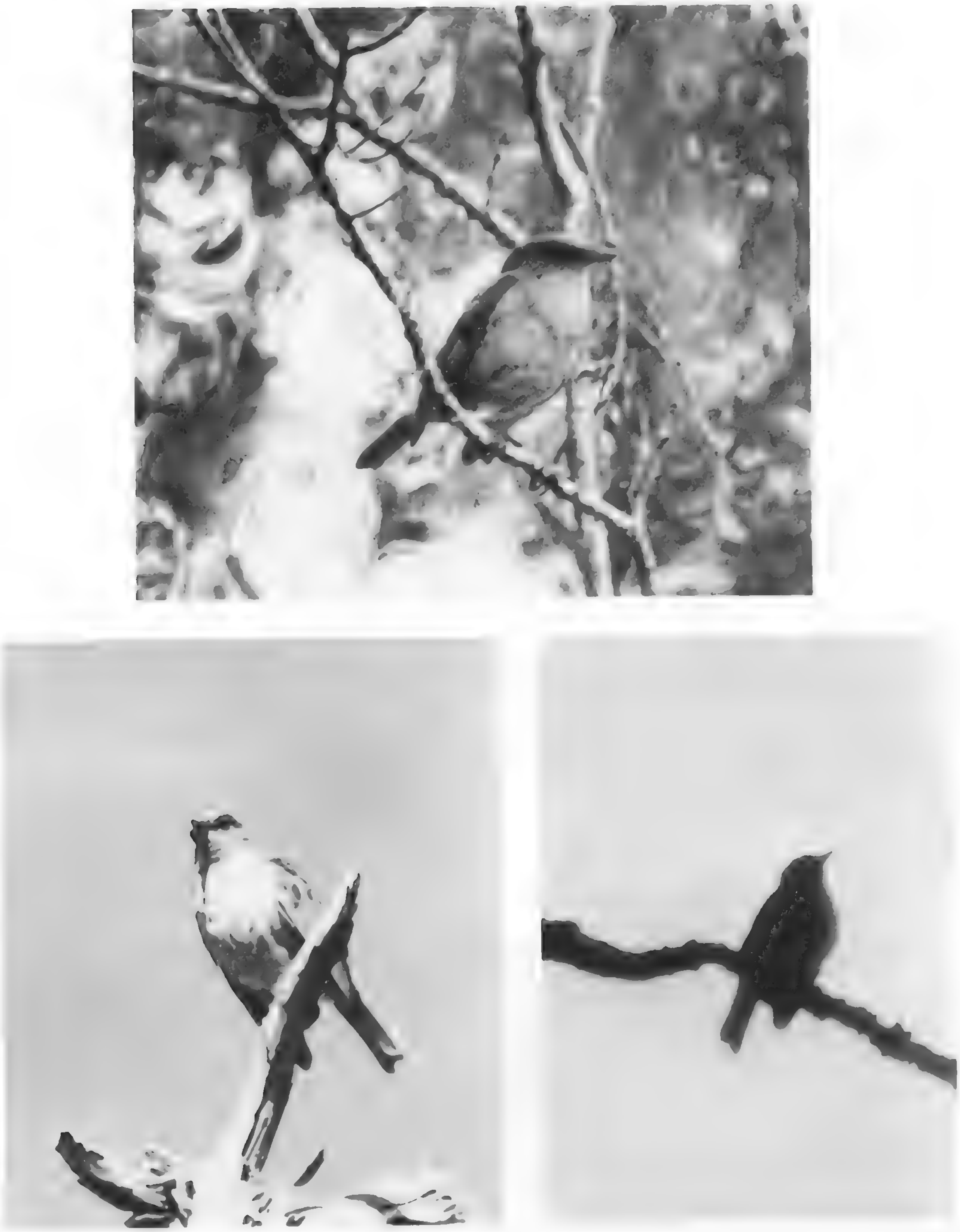


Figure 3. Characteristic postures of the Omao (*Myadestes obscurus*). Photographed at Keauhou Ranch, Island of Hawaii, by the author.

MORPHOLOGY

Bill

Solitaires clearly differ from typical thrushes in the shape of the bill, which is short and broad and resembles those of silky flycatchers (Sibley 1973). This bill shape apparently is an adaptation for combined flycatching and fruit-eating. Bills of Hawaiian thrushes are more variable among themselves than are those of solitaires. The extremes are represented by the two Kauai species. The bill of the larger Kamao (Figure 4, A) is, as Stejneger (1889: 384) states, "identical [to], though somewhat stouter and stronger" than those of solitaires (Figure 4, E-G). The bill of the Puaiohi (Figure 4, D) is the narrowest of all, and resembles the bills of typical thrushes. The morphological divergence of the two Kauai forms may have resulted from competition (Amadon 1947, Ripley 1962), since the isolated forms on Molokai, Lanai, and Hawaii have bills of intermediate shape (Figure 4, B-C). On islands with only one form of thrush, selection has probably favored a more generalized bill structure. Even the insular Cuban (*Myadestes elisabeth*) and Rufous-throated solitaires live alongside (are sympatric with) typical thrushes. In fact, if Kauai had not twice been colonized by thrushes, one that now eats mainly insects and the other mainly fruit, we might expect all *Phaeornis* to have evolved a more generalized bill type. Grant (1965a) has cited several examples of such broadening of feeding niche, accompanied by changes in bill shape, among birds of the Tres Marías Islands off Mexico. Evolution of the bills of Hawaiian thrushes could, of course, have proceeded in either direction, from long and narrow to short and broad, or vice versa. However, the closest resemblance to the bill shape of a mainland thrush is seen in the Kamao, whose bill is proportionately almost identical to the specialized bills of solitaires. I doubt that this bill shape evolved twice among thrushes, particularly in light of the other characters shared by *Phaeornis* and *Myadestes* that set them apart from other members of the family. Thus the divergence from the solitaire bill shape exhibited by the other Hawaiian thrushes in no way argues against considering the two groups congeneric. Such divergence could be predicted from the findings of Schoener (1965), who showed greater variation in bill size among West Indian representatives of several passerine families than among their mainland counterparts. In fact, generic separation of *Phaeornis* and *Myadestes* obscures an important example of evolutionary trends in bill structure in insular members of mainland genera.

Body Proportions

Stejneger (1889) could cite only the different proportions of wing, tail, and legs for making a generic distinction between *Phaeornis* and *Myadestes*. His analysis was based only on a comparison of the Kamao (*P. myadestina*) with several solitaires, but showed that some solitaires differed less from *Phaeornis* in these respects than they did from other *Myadestes*. Table 1 gives the wing/tail ratios of all the species in this complex that I examined. The relatively shorter tails of the Hawaiian birds can be seen as simply the extension of a trend established by the mainland forms. *M. townsendi, M. coloratus, M. genibarbis sibilans,* and *P. lanaiensis* have virtually identical wing/tail ratios; thus the character is useless for defining the two genera. Much greater gaps in the wing/tail ratio cline exist among various species of *Myadestes* than between *P. lanaiensis* and *M. townsendi,* and the

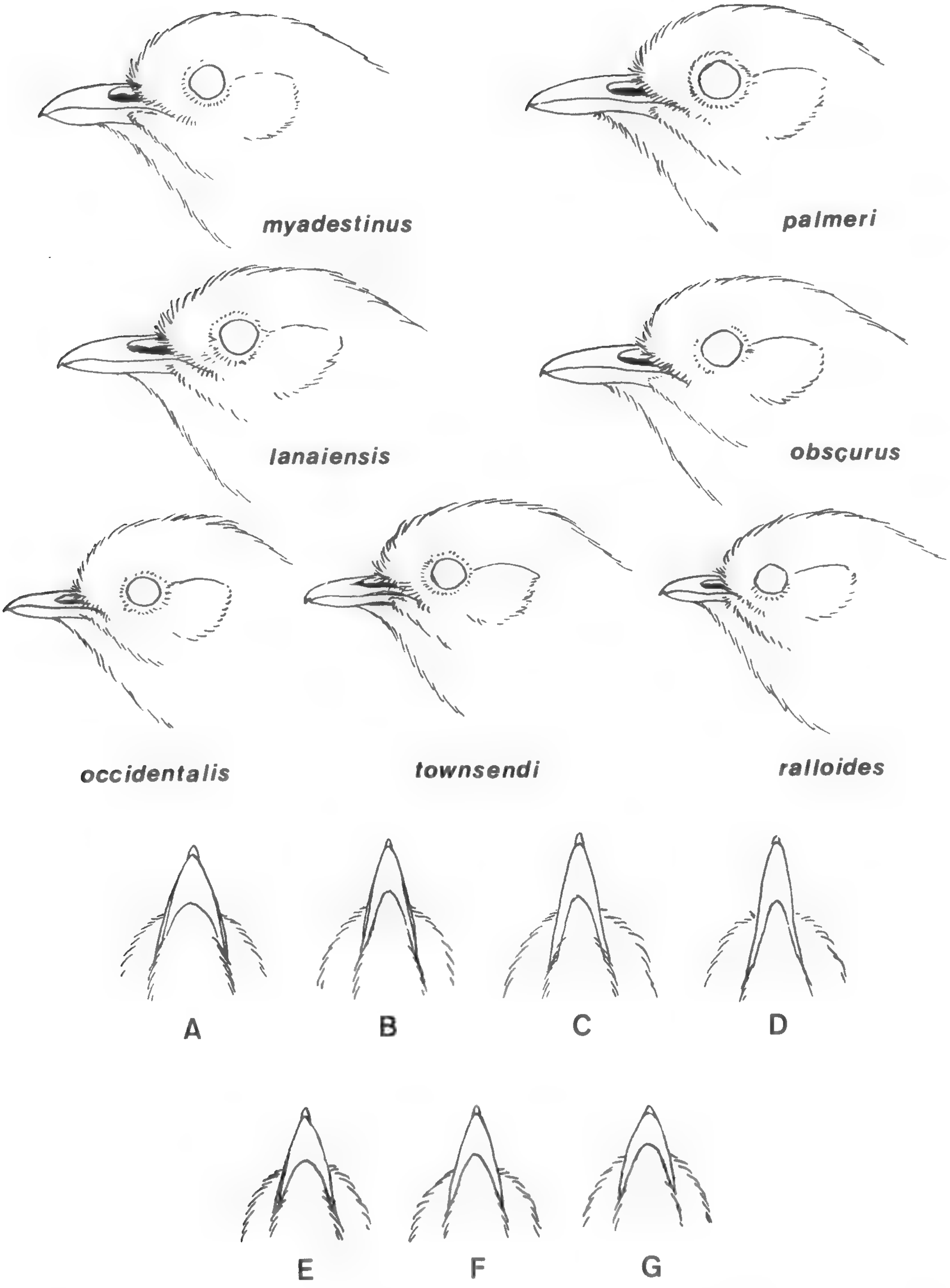


Figure 4. Bills of Hawaiian thrushes and representative solitaires. Ventral views (fourth and fifth rows): Hawaiian forms of *Myadestes* (*"Phaeornis"*) (A) *myadestinus*, (B) *obscurus*, (C) *lanaiensis*, (D) *palmeri;* mainland *Myadestes* (E) *occidentalis* (formerly *obscurus*), (F) *townsendi*, (G) *ralloides*. All to scale.

largest gaps of all occur within the Hawaiian group of species. The wing/tail ratios appear therefore to be following a pattern of divergence from their ancestral type similar to that of bill structure.

Ridgway (1907) used the greater tarsus length of *Phaeornis* as a key character to separate that genus from *Myadestes.* But the longer tarsus of *Phaeornis* is shown by Stejneger's (1889) data to represent just the extension of another morphological cline. A tendency toward greater tarsus length in island representatives of mainland genera has been demonstrated by Grant (1965a, 1966).

Internal Anatomy

Little is known of the internal anatomy of Hawaiian thrushes. Only specimens of the Omao (*P. obscura*) have been available for anatomical study and it is unlikely that the other species can or will ever be obtained because of their rarity or extinction.

Lucas (1894), in comparing skulls of the Omao and the Rufous-throated Solitaire, considered the two genera closely related. Indeed, he usually referred to them collectively when reconciling their placement in the thrush family. Since the Kamao is more solitaire-like in bill shape than the Omao, its skull might well reveal even greater similarities. Planned extraction of skulls from study skins by S. L. Olson (pers. comm.) may fill some of the gaps in our knowledge.

Morioka (1967) divided all thrushes into two groups on the basis of skeletal and muscular features. He found that *Phaeornis* and *Myadestes* belonged to the same group but he placed *Catharus* in the other. Morioka also showed that among the thrushes, only *Phaeornis* and *Myadestes* lack

TABLE 1

Wing and Tail Length Means and Wing/Tail Ratios of Solitaires (*Myadestes*) and Hawaiian Thrushes ("*Phaeornis*")

	N	*Wing (mm)*	*Tail (mm)*	*Wing/Tail ratio*
"Phaeornis"				
palmeri	3	88	57	1.54
obscura	40	102	69	1.47
myadestina	20	106	80	1.33
lanaiensis	21	95	80	1.19
Myadestes				
townsendi	8	116	99	1.17
coloratus	8	88	75	1.17
genibarbis sibilans	6	87	75	1.16
leucogenys	6	104	92	1.13
melanops	8	87	78	1.12
ralloides	8	84	75	1.12
unicolor	8	95	89	1.07
elisabeth	7	89	84	1.06
genibarbis sanctaeluciae	6	92	87	1.06
genibarbis dominicanus	9	92	88	1.05
occidentalis (=obscurus) mainland forms	15	101	96	1.05
genibarbis solitarius	11	91	89	1.02
occidentalis insularis	4	96	96	1.00

ossified nasal septa and alinasal turbinals. Nor did he note any differences between *Phaeornis obscura* and *Myadestes* species that were greater than typical interspecific divergences. Olson (pers. comm.) has compared skulls of both adult and juvenile *Phaeornis* from the island of Hawaii with those of *Myadestes,* and he considers the two groups very similar in general appearance of the skull. Interestingly, he found the skull of a juvenile *Phaeornis* to be more like those of continental *Myadestes* than were those of adults.

Ames's (1975) study of the syrinx revealed another anatomical feature in which *Phaeornis* and *Myadestes* resemble each other but differ from other thrushes. In the Hawaiian birds, the syrinx is of the same unusual type as that of solitaires, but has diverged even further from the typical thrush syrinx.

In summary, the genera *Phaeornis* and *Myadestes* cannot be differentially diagnosed on morphological grounds. They are virtually indistinguishable in plumage, postures, and bill structure, and are similar in cranial and syringeal characters. Furthermore, in all of these characters the two groups share features that are different from those of typical thrushes. But because Ripley's (1962, 1964) classification was based mainly on vocalizations, an examination of those and other behavioral characters is warranted.

VOCALIZATIONS

Calls

Both the Omao and the Kamao utter a low-pitched, inquisitive raspy call that resembles the mewing call of the Gray Catbird (*Dumetella carolinensis*). In the Puaiohi, the homologous call is a harsh, almost toneless hiss. The larger Hawaiian thrushes also give a burry whistled call that sounds like a police whistle. As uttered by the Kamao, both calls are higher-pitched and less raspy than those of the Omao, and the "police whistle" has an ethereal quality produced by double-voicing of the notes. The call of the Rufous-throated Solitaire closely resembles that of the Kamao and has also been described as a police-whistle call (Lack 1976). Some nightingale-thrushes have a cat-like call note (Slud 1964), but none I have heard resemble the low rasp of the Hawaiian thrushes. However, one call of the Black-faced Solitaire sounds very much like the low-pitched Omao call. On the basis of call notes, then, Hawaiian thrushes are more like solitaires than like nightingale-thrushes.

Songs

The thrushes have been considered by most writers to be Hawaii's most skilled native songsters. Their songs differ considerably from island to island (Munro 1960), and thus are difficult to characterize as a group. The song of the Omao is rather unthrushlike and jerky but "pleasing and, at times, sweet" (Henshaw 1902: 29). The segment shown in Figure 5 is typical. The song comprises sharply up-and-down slurred whistles, without double-voicing. It therefore lacks the flutelike quality characteristic of many thrush songs. The song is loud, however, and echoes in the forest to such an extent that clear spectrograms are difficult to obtain. The song of the Kamao is entirely different from that of the Omao and has been described as resembling "that of an English thrush, but ... less powerful" (Palmer *in* Rothschild 1893–1900) and composed "of flute-like double

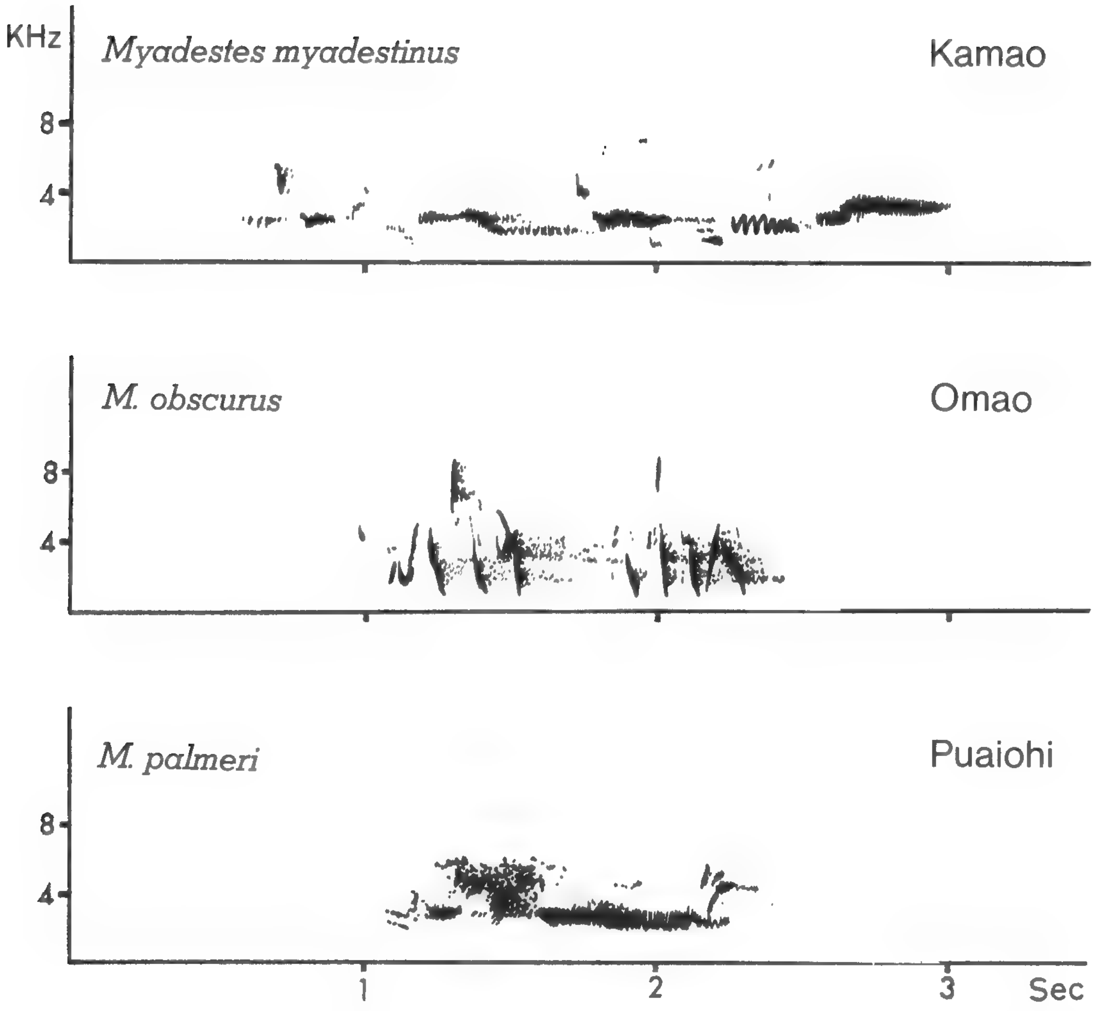


Figure 5. Songs of three species of Hawaiian thrushes. Recording data as follows: Kamao (LNS 5012) by the author, 2 July 1975, Alakai Swamp, Kauai; Omao (LNS 5166) by the author, 17 August 1975, Keauhou Ranch, Hawaii; Puaiohi (LNS 5898) by Gauthey et al. (1968), 1 June 1968, Alakai Swamp, Kauai. These diagrams are ink tracings of spectrograms made on the Spectral Dynamics Model SD301-C Real Time Analyzer with a range of 0–10,000 Hz and a band width of 120 Hz.

notes" (Richardson and Bowles 1964). The double-voicing can be seen in the example given in Figure 5. The song lacks the sharp ascending and descending whistles of the Omao and is characterized by rapid frequency modulations of narrow amplitude that produce a burry quality, like that of some of the call notes. The song of the Puaiohi (as recorded by Gauthey et al. 1968) is much less musical than the songs of the other two Hawaiian thrushes. It is wheezy and high-pitched, like the squeaking of a metal wheel in need of lubrication, but it contains some notes that resemble elements of the Kamao's much longer and more elaborate song. All three known Hawaiian thrush songs are reiterated between pauses of varying length. The examples shown in Figure 5 are single segments extracted from lengthy series of songs and pauses. The Olomao has an "irregular... somewhat jerky, though always melodious" (W. A. Bryan 1908: 174) song on Molokai, but on Lanai it apparently was "no singer at all" (Munro 1960: 74). No recordings exist of the song of the Olomao.

Ripley (1962) claimed that in "song and apparently in habits" Hawaiian thrushes were "far closer to *Catharus* especially the central American nightingale-thrush group" than to *Myadestes*. Obviously, he considered the songs of solitaires to be noticeably different from those of nightingale-thrushes. I listened to recorded examples of the songs of five species of *Myadestes,* the four temperate zone *Catharus,* and five species of nightingale-thrush. In general, and to my ears, *Catharus* songs are simpler than those of solitaires and the temperate zone species have longer more complex songs than do the nightingale-thrushes. Despite these generalizations, songs of some nightingale-thrushes closely resemble the songs of some solitaires. Spotted Nightingale-thrush (*C. dryas*) and Black-faced Solitaire songs can hardly be distinguished. Thus, although the two groups can be generally characterized on the basis of song, the differences are neither clear-cut nor consistent and are, in my opinion, of only limited taxonomic value. The song of the Kamao resembles that of Townsend's Solitaire more than it does that of any other mainland species, but this may or may not be important.

The behavior associated with singing may provide more phylogenetically significant data than does song alone. Solitaires and Hawaiian thrushes choose song perches high in the forest canopy (Bent 1948, Skutch 1967, pers. obs.), whereas *Catharus* thrushes usually sing on or near the ground (Bent 1949, Skutch 1960). Singing in flight is unusual among thrushes in general (Skutch 1960), but almost all writers have mentioned that Hawaiian thrushes sometimes sing on the wing. I have seen this behavior in both the Kamao and Omao. The birds often end a bout of singing in the treetops with an upward flight, a brief period of singing on the wing or "skylarking," and a sudden dive into the forest understory. Similar behavior has been noted in the Puaiohi (Perkins 1903). Townsend's Solitaire (Bent 1949, Bailey and Niedrach 1965) and the Brown-backed Solitaire (Gunn and Gulledge 1977) have a virtually identical song flight. In the genus *Catharus,* only the Gray-cheeked Thrush is known to have a song flight, which is apparently not similar to the song flights of solitaires and Hawaiian thrushes (Bent 1949).

Nesting

A possible Olomao nest in a fork about 9 m (30 ft) high in an ohia-lehua tree was reported by W. A. Bryan (1908), but the first confirmed nest of a Hawaiian thrush was that of an Omao (Berger 1969). It was located about 1.3 m (4.3 ft) above the ground against the trunk of a tree fern. More recently, other Omao nests have been found in niches or cavities in trees (van Riper and Scott 1979). All were bulky constructions of various plant materials. No nests of Hawaiian thrushes have yet been found on the ground, but the alpine population of the Omao would have to use terrestrial sites.

The best-known nest of the genus *Myadestes* is that of Townsend's Solitaire. Often the nest is built on or near the ground, frequently in a recess in a steep bank with an overhanging shelter (Bent 1949). Similar nest sites have been reported for the Cuban and Rufous-throated solitaires of the West Indies (Bond 1974), for the Black-faced and Brown-backed (*M. occidentalis = obscurus;* see beyond) solitaires in Central America (Skutch 1967), and for the Andean Solitaire in Colombia (Wallace 1965). Other low sites include a nook in the side of a leaning moss-covered tree (Skutch 1967) and a cavity in a stub or the heart of a tree fern (Bond 1974). The Rufous-throated Solitaire sometimes chooses higher nest sites in trees, such as in a bromeliad about 15 m (49 ft) above the ground or in a tree fork at 4 m (13 ft) (Cruz 1976). These nests are all bulky and structurally similar to those of

Hawaiian thrushes (Berger 1969, van Riper and Scott 1979).

Nightingale-thrushes build small compact nests in low shrubbery (Skutch 1960, Wallace 1965), and the temperate *Catharus* often nest also on the ground but never in cavities or niches (Bent 1949, Harrison 1978). These nests bear little similarity to those of Hawaiian thrushes.

The eggs of solitaires are white to pale blue, liberally spotted with reddish brown, with the spots often concentrated toward the larger end (Skutch 1967, Bent 1949). The eggs of Townsend's Solitaire are "entirely different from the eggs of other North American thrushes" (Bent 1949: 320) as can be readily seen in a recently published plate (Harrison 1978). Thus the similarity of the eggs of the Omao and Puaiohi (as described by Berger 1981) to those of solitaires may be noteworthy. Lack (1958), however, considered egg color useless as an indicator of relationships among thrushes.

TAXONOMY

Because no morphological, behavioral, or ecological characters distinguish *Phaeornis* from *Myadestes,* I see no justification for maintaining the two as separate genera. I therefore formally propose *Phaeornis* Sclater 1859 as a junior synonym of *Myadestes* Swainson 1838.

One consequence of acknowledging that Hawaiian thrushes are solitaires is that the long-established scientific name of the Brown-backed Solitaire, *M. obscurus* Lafresnaye 1839, must yield to the priority of *Myadestes obscurus* (Gmelin) 1789, now the name of the Omao. According to nomenclatural rules, the Brown-backed Solitaire will now be called *M. occidentalis* Stejneger 1882, and the former nominate subspecies must be renamed (Pratt in press).

POSSIBLE ANCESTRY

Townsend's Solitaire is more like the Hawaiian thrushes than is any other mainland *Myadestes.* Its song resembles that of the Kamao, its wing/tail ratio is almost identical to that of the Olomao, and it exhibits alpine adaptations similar to those of the Mauna Loa population of the Omao. These characteristics suggest that the Hawaiian thrushes as a group may be descended from the same ancestral species as is *Myadestes townsendi.* Townsend's is also the only migratory solitaire and thus represents the evolutionary line most likely to colonize a remote island; during migration Townsend's Solitaires sometimes forsake their solitary habits and gather in aggregations or flocks (Bent 1949, Phillips et al. 1964), ideal for island colonizations. In winter, Townsend's Solitaires also wander widely in "family groups," following variable food supplies (Bent 1949).

SPECIATION AMONG HAWAIIAN SOLITAIRES

The key to the interrelationships of the Hawaiian solitaires lies in determining which of the two Kauai species is the more recent colonizer. Amadon (1947) proposed a scenario in which the Puaiohi (*M. palmeri*) reached Kauai first and, because of the relative isolation of that island, diverged to the species level. A second invasion by the same ancestral species then occurred, giving rise to the Kamao (*M. myadestinus*). Amadon considered the Kauai example to be a typical double-invasion phenomenon, with subsequent character displacement. However, in bill shape, diet, and vocalizations the Kamao is the most clearly myadestine member of the Hawaiian solitaire group, whereas the Puaiohi is the most divergent in these same characters. For Amadon's hypothesis to be valid, the ancestral characters of the Kamao would have to have been lost and then regained after the second invasion of Kauai.

I favor a simpler scenario that would have the Kamao retaining its solitaire-like characters throughout its history. Thus it would represent a direct link to the mainland ancestor of all Hawaiian *Myadestes*. Kauai may well have been the site of the first landfall by *Myadestes* in the islands, since it is farther north and therefore closer to a possible source area (recall that modern Townsend's Solitaires breed to tree line in central Alaska). All historical records of continental passerines in the archipelago have come from the small islands that lie north and west of Kauai; none have ever been recorded among the main islands (Berger 1981). Modern theories of island colonization suggest that invading species usually spread rapidly throughout an archipelago before undergoing major divergence (Ricklefs and Cox 1972). Thus a single species of *Myadestes* may originally have occurred throughout the islands. At least one of the island forms diverged sufficiently to become a new species, and then reinvaded Kauai to share it successfully with the first colonizer. Thus the Kauai example is not a typical double-invasion phenomenon as Amadon (1947) suggested, because the two *Myadestes* are from different source areas, one more-or-less directly from the mainland, the other from within the archipelago. (The remoteness of the Hawaiian Islands makes two invasions from the mainland highly unlikely.) I believe the Puaiohi represents the second invader. Its longer and narrower bill, insectivorous diet, and distinct vocalizations simply extend the trends away from continental characteristics seen in the solitaires of the other islands.

If my scenario is correct, then logically a minimum of three solitaire species must be (or have been) present in Hawaii, unless the Puaiohi is conspecific with the allopatric forms. No one has ever suggested the latter possibility, because the Puaiohi is so distinctive within the complex. Most authors have overlooked the fact that the Kamao is equally distinctive, particularly with regard to vocalizations.

Vocalization Experiments

To test the possibility that potential reproductive isolating mechanisms exist among the Hawaiian *Myadestes* that live on separate islands, I conducted a series of vocal playback experiments on the island of Hawaii. On 28 and 29 April 1977 I visited Keauhou Ranch (which lies between Kilauea Forest Reserve and Hawaii Volcanoes National Park) where Omao were abundant and many were singing vigorously. I had prepared tapes of Kamao call notes and songs from recordings I made in 1975 on Kauai, and also tapes of homologous vocalizations of the Omao from Keauhou Ranch. Before I began experimenting with the Kauai tapes, I tested responsiveness of singing Omao to playbacks of previously recorded Omao songs and calls.

The raspy, cat-like Omao call elicited no response whatever. Singing birds continued uninterrupted, and birds giving the same call did not alter their behavior when the tape was played. The higher-pitched call was also ignored. This latter result was surprising in light of Perkins' (1903) statement that Omao could be attracted by imitation of that call. Response to the Omao song was, however, immediate and obvious. First the experimental subject, singing vigorously, flew upward from its perch and then dived into the forest understory near the playback speaker. Then the Omao approached silently in a series of short flights as if attempting a surreptitious investigation. When only a short distance from the speaker, the bird stared intently at the sound source, but did not appear agitated. In fact, the wing-shivering, characteristic of Hawaiian thrushes, ceased during the bird's approach to the recorded sound. The bird remained, seemingly oblivious to human presence, as long as the playback continued. When the tape ended, the Omao flew back into the canopy and resumed singing.

Having established that the birds were responsive to song playback, I began playing the Kamao tape first, followed by the Omao recordings—a method similar to that used by Raitt and Hardy (1970) in their study of two Mexican species of *Catharus.* In the first experiment I played the Kamao tape for an apparently territorial, vigorously singing Omao. Neither the two different call notes nor the complex Kamao song (Figure 5) elicited any response, or even any indication that the bird heard the tape. The subject's vocalizations continued until the taped Omao song began. The bird then ceased singing abruptly and flew directly to an open perch about 4 m (13 ft) above the playback speaker. Its approach to the speaker then closely matched that previously described. I conducted nine such playback experiments during the two-day period, involving nine different individuals. None of these birds responded in any way to recordings of the Kamao. Seven responded vigorously to subsequent presentation of the Omao song; two others responded to neither tape. At the time I did not have a recording of the Puaiohi song, but it is so different from the songs of the Omao and Kamao that response to it by either of those species seems unlikely.

Conclusions

Lanyon (1967) interpreted the same kinds of responses to taped vocalizations by flycatchers as indicating that forms with nonoverlapping ranges were separate species, although they were morphologically similar. Like flychatchers, many thrush species are similar in appearance but differ vocally (Dilger 1956, Raitt and Hardy 1970). Thus it is reasonable to interpret vocal differences among allopatric Hawaiian solitaires as potential isolating mechanisms, and I conclude that the Puaiohi, the Omao, and the Kamao are distinct species.

The solitaires of Oahu, Molokai, and Lanai are problematical. The Lanai and Molokai birds were originally considered a single taxon (*lanaiensis*) and bore the single native name, Olomao. W. A. Bryan (1908) gave the epithet *rutha* to the Molokai population on the basis of slight differences in color and measurements. Later Munro (1960), with years of field experience on Lanai, pointed out that the two forms differed vocally, in that *lanaiensis* did not sing at all but gave only call notes. I re-examined Bryan's type series of *rutha* in the Bishop Museum, and compared the skins with more recently collected specimens from Lanai. I cannot see the color differences he noted. Perhaps the apparent differences were artifacts resulting from the comparison of a then–fresh series from Molokai with older Lanai specimens. Nor could I detect any important differences in measurements of the two populations. Thus to distinguish the two taxa, we are left only with Munro's (1960) report of the lack of song in *lanaiensis.*

Molokai, Lanai, and Maui were united during the last glaciation and may have separated as recently as 10,000 years ago (Juvik and Austring 1979). Probably a single form of *Myadestes* inhabited the conjoined island, and thus the populations on Lanai and Molokai have had relatively little time for differentiation. I believe *rutha* and *lanaiensis* must be considered the same species; their differing vocal behavior, however, justifies recognizing them as subspecies. But should they be considered conspecific with any of the other Hawaiian *Myadestes?* The Olomao (*lanaiensis* + *rutha*) is as distinct morphologically in the complex as are the Omao, Kamao, and Puaiohi. Earlier writers considered the song (on Molokai at least) distinctive as well. Thus I believe the best course is to recognize the Olomao as a separate species, *M. lanaiensis,* with subspecies on Lanai (*M. l. lanaiensis*) and on Molokai (*M. l. rutha*).

The extinct Amaui of Oahu conceivably could have been conspecific with one of the three certain species, or with the Molokai and Lanai forms. In the absence of specimens, its status must be considered hypothetical. Perhaps recently discovered fossil solitaires from Oahu (S. L. Olson pers. comm.) will help to solve the problem. In the meantime, I recommend that the Amaui appear in checklists as a questionable species *Myadestes ?oahensis.*

The Hawaiian solitaires (thrushes) are an excellent example of island evolution. Although they retain enough of their ancestral characters to indicate their relationships, they exhibit all levels of speciation, and have begun the process of interisland cross-colonization that has led to spectacular adaptive radiations in such groups as the Hawaiian honeycreepers. The solitaires are thus instructive in demonstrating how such evolutionary phenomena began.

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MUSEUM OF ZOOLOGY
LOUISIANA STATE UNIVERSITY
BATON ROUGE, LOUISIANA 70893

Pintail, *Anas acuta.* Painting by George E. Gilbert, courtesy of John Steed.

BIOLOGY AND CONSERVATION OF THE BAHAMA PARROT

Noel F. R. Snyder, Warren B. King, and Cameron B. Kepler

The Bahama Parrot (*Amazona leucocephala bahamensis*) was once abundant and widespread within its range. Christopher Columbus found parrots on all the large Bahama Islands he visited in 1492, and described vast flocks that obscured the sun on Crooked Island (Morison 1963). Parrots were probably originally present on all the major islands of the Bahama archipelago, although documented records exist only for Abaco, New Providence, San Salvador, Long, Crooked, Acklins, and Great Inagua islands, and Long Cay (Bond 1956, Brodkorb 1959, Morison 1963). A subspecies of the Cuban Parrot, this form is the only psittacid that occurs in the Bahamas.

Like all West Indian parrots, the Bahama bird has not prospered in contact with European man. By the 1940's it was no longer present on any of the islands where Columbus had seen it, and could be found only on Abaco, Acklins, and Great Inagua. The Aklins population was extirpated shortly thereafter, and today the parrot persists only on Abaco and Great Inagua, at the northern and southern limits of its known former range (Figure 1).

The Bahama Parrot has been recognized as endangered by the International Union for the Conservation of Nature since 1966 (Vincent 1966) and by the U.S. Department of Interior since 1970 (U.S. Bur. Sport Fish. & Wildl. 1970), yet little is known of its precise status and virtually nothing has been published about its biology. To remedy this state of affairs, we made three trips to Abaco in 1976 and 1977 and one to Great Inagua in 1979. The first visit, by W. King from 18 to 22 February 1976, and the second, by C. and A. Kepler and N. Snyder from 14 to 19 November 1976, were primarily to estimate the size of the Abaco parrot population. The third Abaco trip, by J. Grantham, W. King, M. and Y. Segnestam, D. Shaw, N. Snyder, and R. Warner, from 16 to 28 May 1977, yielded data on the early breeding cycle stages. From 26 to 31 March 1979 H. and N. Snyder made general observations of the parrots on Great Inagua.

VEGETATION, CLIMATE, AND GEOGRAPHY

Abaco

The second largest of the Bahamas (1,681 km^2 [649 mi^2]) is actually two islands, Great and Little Abaco, now linked by a short bridge (Figure 2). Like the rest of the Bahamas, Abaco is relatively flat and composed of limestone. Low ridges reaching a maximum elevation of 37 m (120

The Bahama Parrot, *Amazona leucocephala bahamensis*. Photographed on Great Inagua Island by N. F. R. Snyder.

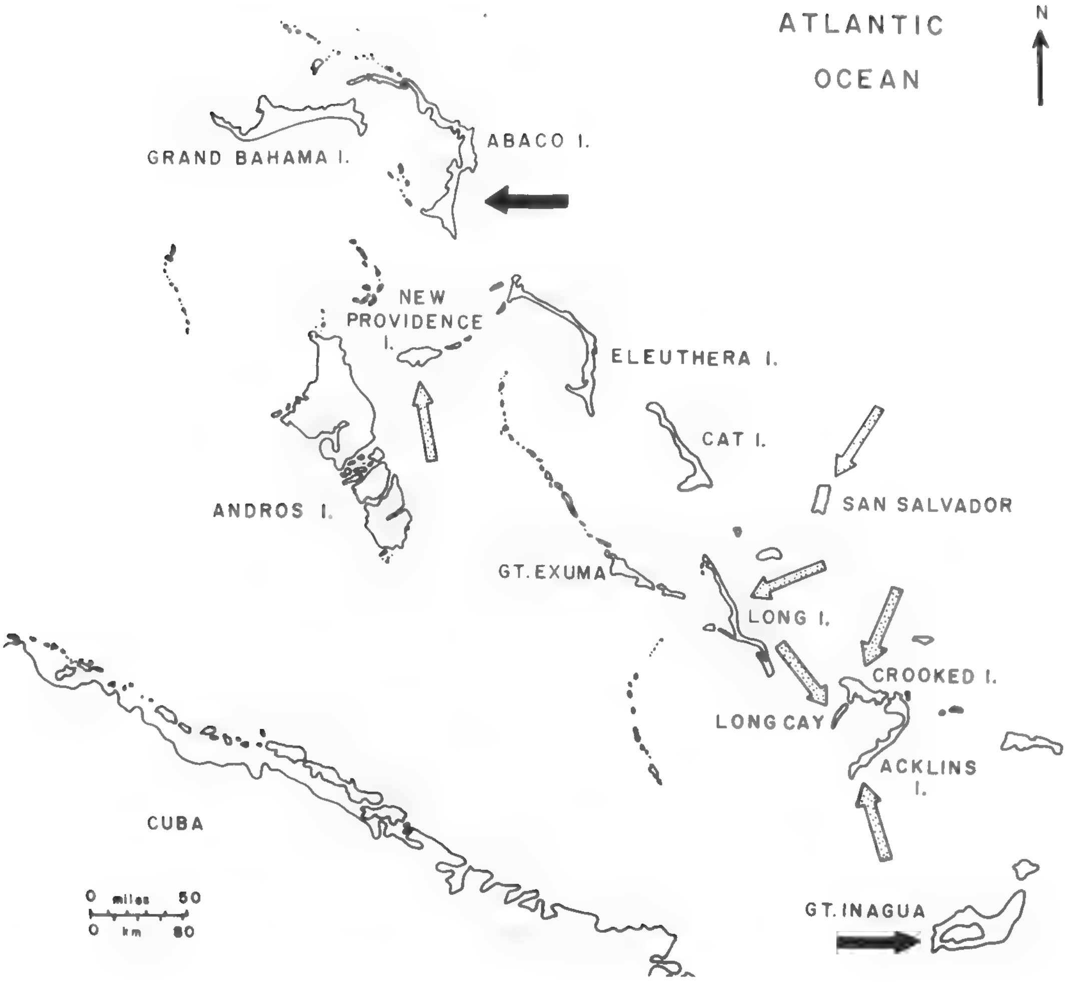

Figure 1. Range of the Bahama Parrot. Solid arrows indicate present range; stippled arrows, islands where parrots are known to have been extirpated.

ft) extend along the eastern (windward) coast and transversely across the island in several places. The island's climate is subtropical and fairly dry; annual rainfall is variable but averages 154.4 cm (60.8 in.) at Green Turtle Cay, and temperatures are generally mild with monthly means ranging from 21° to 27°C (70–81°F) (Commonwealth of the Bahamas 1976, Henry 1974). Rainfall peaks in June and again in September and October. Snow was unknown until the severe winter of 1976–1977 when a few flakes fell, amazing the residents.

Abaco is sparsely and unevenly inhabited. In 1970 the population of 6,501 people was primarily concentrated in the Marsh Harbour area, near the midpoint of the island. Most settlements are on the windward coast or on small offshore (eastern) cays; the interior of the island is almost uninhabited.

With the other major northern islands of Grand Bahama, Andros, and New Providence, Abaco shares a dominant and prolific growth of pine, *Pinus caribaea.* In general, as one travels from east to west across the long narrow island, one finds first a thin coastal strip of dunes covered by sedges, coconut palms (*Cocos nucifera*), casuarinas (*Casuarina litorea*), and other wind- and salt-spray-tolerant species; then a strip of native evergreen hardwood, "coppice," which is dramatically windpruned and varies in width from a few meters to 2 km (1 mi) or more; then a broad expanse of pine barrens or "yards"; and, finally, mangrove flats or, in some areas, a leeward strip of coppice.

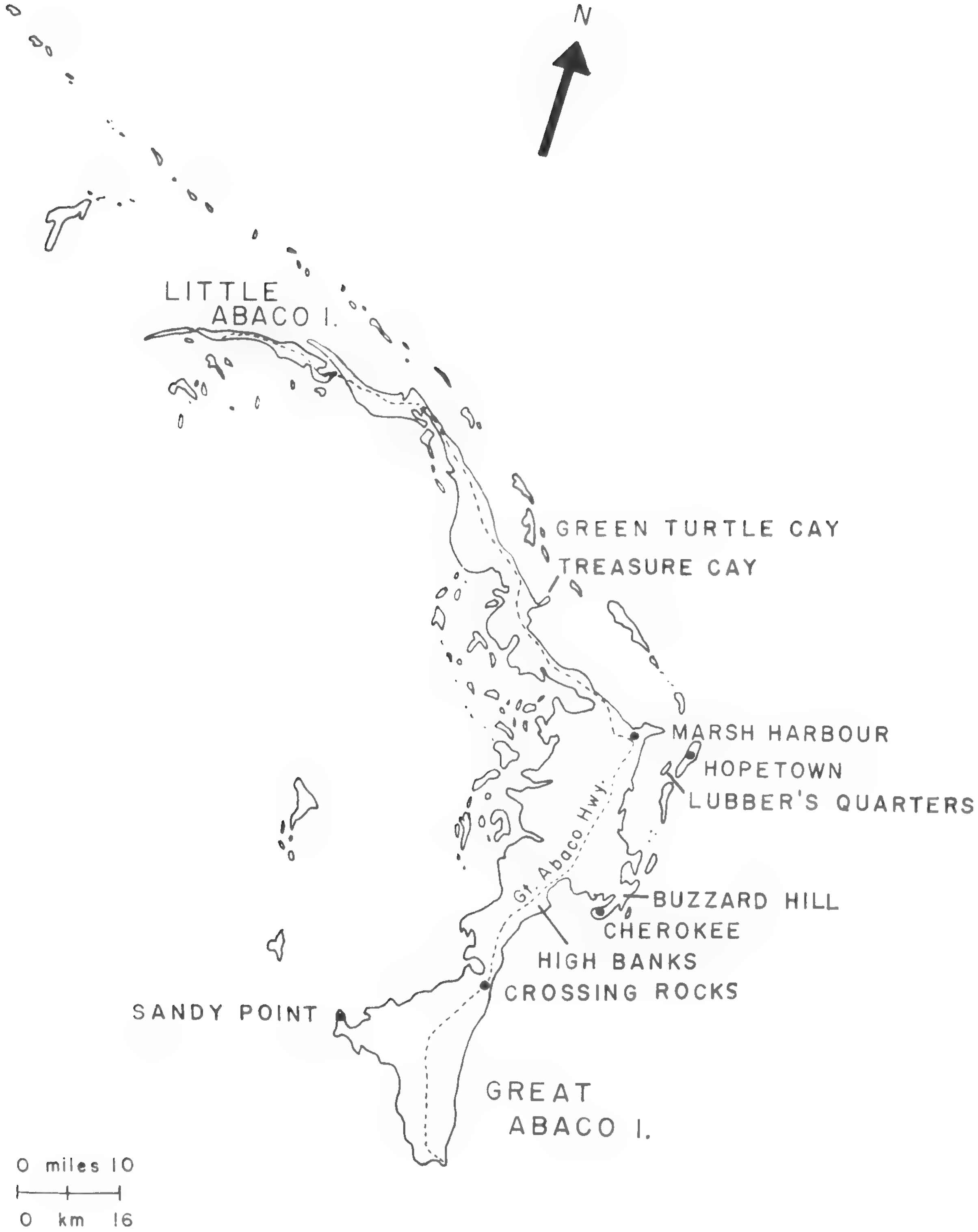

Figure 2. Great and Little Abaco islands, Bahamas.

Between 1905 and 1944 a local lumbering company cut over essentially all the pinelands on Abaco, taking trees 15 cm (6 in.) and larger in diameter (Henry 1974). In 1959 an American company began a more systematic pulpwood operation. To facilitate the cutting, it built the Great Abaco Highway, which extends the length of the island, and a network of connecting feeder roads. This time the 15-cm restriction was not in effect, but 12 seed trees were left per hectare (2.5 acres). Cutting operations were completed by 1967, leaving intact only a few relict stands of old-growth pine.

North of Marsh Harbour the pines have regenerated well since the last cutting. Immediately south (between Marsh Harbour and Crossing Rocks) there is fair-to-good regeneration, but a tract of 178.2 km^2 (68.7 mi^2) has been cleared and planted in sugar cane. South of Crossing Rocks the pines are doing poorly. In early September 1965, when lumbering was nearly completed, the center of Hurricane Betsy passed the southernmost tip of the island. Winds up to 286 kmph (178 mph) were recorded as far north as Hopetown, and many of the seed trees were leveled. Of those still standing, many were sufficiently damaged that they were later lost to outbreaks of bark beetles and to fire. The result was nearly total destruction of the potential for natural pine regeneration. The bulk of the region has been taken over by low scrub. Aside from lumbering, the southern third of the island has been little disturbed by man, and despite the recent devastation it remains the primary stronghold of the Bahama Parrot on Abaco.

Great Inagua

Almost the same size in land area (1,544 km^2 [596 mi^2]) as Abaco, Great Inagua is more compact in shape (Figure 3). Its most outstanding geographical feature is a large interior lagoon of 212 km^2 (82 mi^2) that has been extensively diked into salt evaporation pans. There are also several smaller lakes with associated inland mangrove flats. The interior of the island supports large numbers of nesting American Flamingos (*Phoenicopterus ruber*), Roseate Spoonbills (*Ajaia ajaja*), Reddish Egrets (*Dichromanassa rufescens*), and other waterbirds. The dry areas are covered by second- or third-growth low scrub or dense coppice with few large trees; *Pinus caribaea* is absent. Except for slash-and-burn agriculture, and some cutting of the more valuable woods such as lignum vitae (*Guaiacum sanctum*), the composition of the island's vegetation has been relatively little changed by man. About 743 km^2 (286 mi^2) of the island is under lease by the Bahamas National Trust as a wildlife sanctuary, principally to protect the flamingos. Most of the remainder of the island is a *de facto* preserve because it is so difficult of access by land or water. Great Inagua is largely ringed with dangerous reefs and shallow water.

The human population of Inagua numbered only 1,109 in 1970 and is almost entirely concentrated in Matthew Town, on the southwestern end of the island. Historically the population was larger and more dispersed in coastal settlements. The island's economy is based on salt harvest rather than fishing, agriculture, lumbering, and tourism as on Abaco. Roads are few, consisting largely of a shore road along the west and south coasts and of dike roads in the central lagoon.

In geology Great Inagua—a low limestone island—is similar to Abaco, but it is much drier. The mean annual rainfall in Matthew Town is

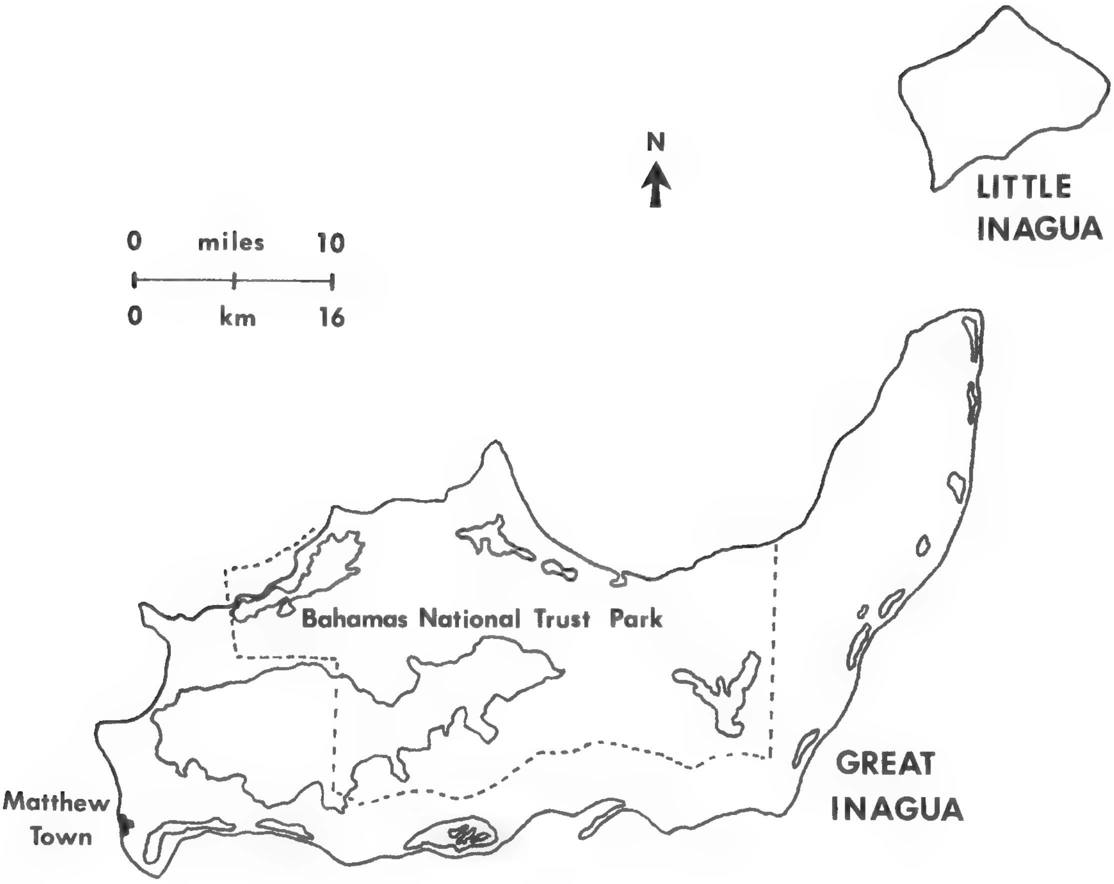

Figure 3. Great and Little Inagua islands, Bahamas.

69.6 cm (27.4 in.), with peaks in May and September-October. The temperature is somewhat warmer, with monthly means ranging between 24° and 29°C (75°–84°F). Parrots are found islandwide, but are patchy in distribution. They may also visit nearby Little Inagua; Ed Haxby, a resident of Great Inagua, saw them on Little Inagua in the late 1970's, but the species has not been recorded there by other recent observers.

POPULATION ESTIMATES

In February 1976 the parrots of southern Abaco were concentrated along the inner edge of the coppice bordering on remnants of the former pine yards. Here the birds roosted communally at night and spread out in groups during the day, to feed in nearby coppice or pines. This distribution was also characteristic of the parrots during November 1976, thus permitting a fairly comprehensive census. Working from 14 to 19 November along the pine-coppice interface, we made morning and evening counts of parrots leaving or entering their roosts. Three observers for each count were spaced at about 1.6 km (1 mi) intervals because flying and vocalizing parrots are detectable up to approximately 0.8 km. Evening observations were generally made from 1600 until dark, morning observations from first light to 0730 or 0800. Duplicate sightings of birds were eliminated by comparing times and directions of flights between adjacent stations.

Absence of good observation points left uncensused about 9 km (5.6 mi) of the main pine-coppice border south of Crossing Rocks; otherwise we covered 24 km (15 mi) of border. We also made counts from four stations in the inland pine yards, two stations wholely within the coppice, and one overlooking a region of coastal mangroves. A few stations were manned more than once, and counts were comparable in the replicates.

We counted 240 to 276 parrots in the region south of Crossing Rocks. Assuming parrots were equally abundant in censused and uncensused regions of pine-coppice border, we estimated from 325 to 375 individuals for southern Abaco.

How closely this estimate approached the actual population size depends on the extent to which all parrots were roosting in the pine-coppice border. Although we may have counted nearly all the parrots in southern Abaco, we hasten to point out that we could have missed many birds if any significant parrot roosts were in central regions of coppice or pine. We saw only one parrot, however, at the four observation stations in the interior pine yards, and the occupied pine area contained a coppice island. Moreover, in extensive reconnaissance of other pinelands during mid-day, we never encountered parrots. It was more difficult to ascertain occupancy of the extremely dense coppice interior; the coppice was laborious to move through and had few natural overlooks. We made only one excursion through this zone to the windward coast and neither saw nor heard parrots. We did observe 10 to 16 parrots from one of two stations within extensive coppice at the southern end of the island, and these birds were about 1 km (0.6 mi) from pines. We do not know whether parrots were also roosting in other central regions of coppice; uncounted birds in this habitat probably represent the major error in the census. We saw no parrots in the mangroves, nor are there any recent reports of parrot roosts there, although we know of one nest on the fringe of mangroves (Clarke Carraway pers. comm.).

All our local contacts on Abaco said that most parrots were to be found south of Crossing Rocks, although at least a few occurred locally, north to Marsh Harbour. Our search in the middle regions of the island was limited to three stations just north of Crossing Rocks, where we found only two or three parrots. According to John Roberts, a resident of Marsh Harbour, parrots could be seen north of Treasure Cay 25 to 40 years ago, but there have been no confirmed recent reports from the northern part of the island. Sightings in 1974 and 1975 for the central part have consistently involved only small groups of parrots, suggesting a population considerably smaller than that found in southern Abaco. A rough estimate of 100 birds for this region might not be too far from the mark. Thus the total population for the island very likely is somewhere between a minimum of about 450 birds and a less-well-defined maximum of 650 to 800 individuals.

The recent sightings in the Marsh Harbour area have been the first in many years, and most residents we interviewed believed the parrots had been increasing to some extent in the last 10 to 15 years. In the early 1960's the population apparently was hit heavily by several stresses—(1) the widespread destruction of pines by lumbering, (2) Hurricane Betsy in 1965, and (3) considerable shooting after the construction of lumber roads. In 1952 the Bahamian government set a $500 fine for molesting parrots. In time this law has become widely respected and may be a major factor in the apparent recent increase in the parrot population.

The number of parrots on Great Inagua is uncertain, although it probably is larger than that on Abaco. The paucity of roads on Inagua makes censusing of the species very difficult, and we made no attempts to

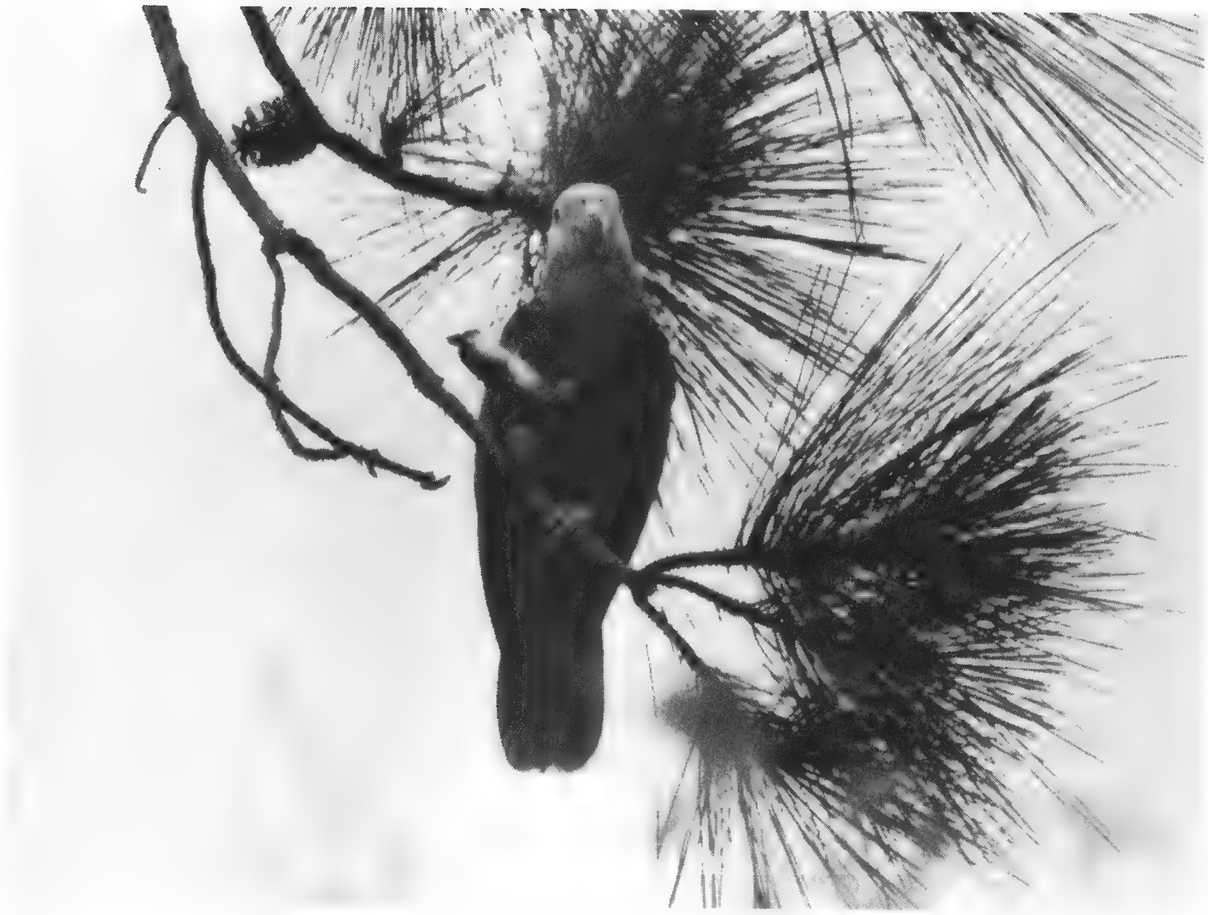

Figure 4. Bahama Parrot feeding on green cone of *Pinus caribaea*. Photo by M. Segnestam, by permission.

do so during our short visit. Although we saw only 70 to 80 parrots in three locations during the five days we were on the island, we covered only a tiny fraction of the island's interior. We learned from our hosts, James and Samuel Nixon of the Bahamas National Trust and Alexander Sprunt IV of the National Audubon Society, of recent sightings of the species from a variety of locations all over the island. Some of the flocks seen in recent years by the Nixon brothers, about the only Inaguans who visit the interior often, must have included hundreds of birds.

FEEDING HABITS

During all three trips to Abaco we were impressed by the apparent abundance of potential plant foods for parrots, both in the pine yards and the coppice. Several types of fruits were conspicuous, and the birds seemed catholic in their tastes. Most feeding records (Table 1) were for *Pinus caribaea* cones. Generally the parrots ate the inner portions of green unopened cones (Figure 4), but we twice saw them working on older, opened cones. The toughness of this diet led us initially to speculate that the large bill of the Bahama Parrot, relative to other subspecies of *Amazona leucocephala* (Table 2), might be related to feeding on pinecones, much as the large bill of the Thick-billed parrot (*Rhynchopsitta pachyrhyncha*) appears to be an adaptation to such food. Bills of the Abaco population, however, are about the same size as those of the Inagua population, and considerably smaller than bills of the now-extirpated Acklins Island birds (Table 2). Both the latter islands have always lacked pines, at least in historical times, so the pinecone hypothesis is at best only part of the story.

TABLE 1

Feeding Records for the Bahama Parrot, 1976–1979

Plant	*Date*	*Observer*[1]	*No. of parrots*	*Comments*
Abaco:				
Pinus caribaea	May 19, 1977	N. S.	2	old cones
"	"	"	2[2]	old cones
"	"	J. G.	1	green cone
"	"	"	1	age of cone?
"	"	W. K.	1	green cones
"	May 22, 1977	N. S.	1	green cones
"	May 23, 1977	"	1	green cones
"	"	"	1[2]	green cones
"	May 24, 1977	W. K.	1	age of cones?
"	"	M. S.	1	green cone
Cassytha filiformis	May 22, 1977	R. W.	4	stems
"	May 26, 1977	N. S. et al.	2	stems
Acacia choriophylla	May 17, 1977	W. K.	1	seeds
"	May 23, 1977	N. S.	1	seeds
Tabebuia bahamensis	May 26, 1977	N. S. et al.	2	seeds
Bursera simaruba	May 17, 1977	W. K.	2	fruits
Swietenia mahagoni	Nov. 16, 1976	N. S.	3+	seeds
Sabal palmetto	Nov. 18, 1976	N. S.	3+	fruits
Great Inagua:				
Swietenia mahagoni	Mar. 28, 1979	N. S.	8	seeds
"	"	H. S.	3	seeds
Coccothrinax argentata	Mar. 30, 1979	N. S., H. S.	12+	fruits
Conocarpus erectus	"	H. S.	8	seeds

[1] Observers: Noel Snyder, Jesse Grantham, Warren King, Mats Segnestam, Rick Warner, Helen Snyder.

[2] Different feeding group at different time of day.

Perhaps the most interesting diet components, next to pinecones, are stems of woe (or love) vine (*Cassytha filiformis*), a plant closely resembling dodder (*Cuscuta* sp.). Woe vine is abundant in southern Abaco, completely covering the scrub in many areas. On tasting it, we found it mild and succulent, not unpleasant, but a little gelatinous after chewing.

In addition to the foods recorded in Table 1, we have been told by Abaconians that the parrots commonly feed on wild dilly fruits (*Manilkara bahamensis*), and in 1967 Harold Mayfield (pers. comm.) saw them feeding on fruits of cinnecord (*Acacia choriophylla*). Residents of Crossing Rocks have had some difficulty with parrots coming into gardens to take pigeon peas and beans, just as Cory (1880) reported that Inagua parrots were once a serious pest in cornfields. On Abaco in the summer of 1977 Clarke Carraway (pers. comm.) saw the parrots feeding frequently on fruits of poisonwood (*Metopium toxiferum*), Caribbean pine, and naked wood (*Myrcianthes fragrans*). He also saw them stripping the outer bark off young pines to eat the inner bark, or cambium.

Fruits were not as conspicuously abundant on Great Inagua as on Abaco, but ample food seemed to be available. Besides the feeding records listed in Table 1, Alexander Sprunt told us of seeing Inagua parrots feeding on fruits or seeds of wild tamarind (*Lysiloma latisiliquum*), jumbay (*Leucaena leucocephala*), poisonwood, sea grape (*Coccoloba uvifera*), buttonwood (*Conocarpus erectus*), buffalo top palm (*Thrinax morrisii*), and silver top

TABLE 2

Bill and Wing Measurements (mm) of *Amazona leucocephala* Subspecies

			Bill (Culmen)			*Wing (Chord)*		
Subspecies	*Location*	*Sex*	*No. specimens*	*Length*	*S.D.*	*No. specimens*	*Length*	*S.D.*
bahamensis	All	M	6	28.8	1.83	7	202.6	4.67
		F	15	28.3	2.04	15	199.6	6.21
	Abaco	M	1	29.0	0.00	1	203.0	0.00
		F	8	27.5	1.22	8	198.5	6.73
	Gt. Inagua	M	3	27.3	0.42	3	198.3	2.85
		F	2	27.4	1.56	2	194.3	6.36
	Acklins	M	2	30.9	1.20	3	206.8	1.45
		F	5	30.0	2.44	5	203.4	3.34
leucocephala	East Cuba	M	12	24.6	1.29	12	182.6	6.35
		F	17	24.2	1.14	17	181.2	5.65
palmarum	West Cuba	M	9	25.9	0.74	9	188.0	3.05
		F	3	23.7	2.04	2	184.8	0.21
	Isle of Pines	M	20	26.4	0.76	20	191.3	4.52
		F	18	25.5	0.86	18	187.8	3.31
hesterna	Cayman Brac	M	5	26.1	0.95	5	178.8	3.96
		F	8	25.0	0.58	9	178.8	4.50
caymanensis	Grand Cayman	M	16	25.6	0.81	16	195.6	5.01
		F	8	24.8	0.69	8	192.8	6.52

Note: Specimens measured in The National Museum of Natural History, Philadelphia Academy of Natural Sciences, American Museum of Natural History, Museum of Comparative Zoology, Carnegie Museum of Natural History, and Yale Peabody Museum of Natural History.

palm (*Coccothrinax argentata*). James Nixon has also recorded their feeding on fruits of cinnecord, poisonwood, and dilly.

Like other amazons, Bahama Parrots commonly feed in flocks. This behavior could relate to efficiency in foraging, detection of predators, or to a combination of these and other factors (Powell 1974, Snyder et al. MS). We sometimes saw what appeared to be sentinel behavior in members of feeding flocks, and we are inclined to believe that avoidance of predators (especially of Red-tailed Hawks, *Buteo jamaicensis,* and wintering Peregrine Falcons, *Falco peregrinus*) may be the primary factor leading to group foraging. At least during our visits, flocking probably was not important in improving efficiency of finding the widespread and abundant food.

REPRODUCTIVE BIOLOGY

Nest Sites

Unlike any other New World psittacids, Bahama Parrots on Abaco regularly nest in holes in the ground. These holes are natural solution cavities in the limestone bedrock. In some places holes are abundant enough to make walking hazardous; in others they are scarce. During the May 1977 trip we found the parrots were largely concentrated in regions with abundant underground cavities.

In other parts of the world, the only parrots known to nest in subterranean holes are the Kea (*Nestor notabilis*) and Kakapo (*Strigops habroptilus*) of New Zealand, the Antipodes Island Green Parakeet (*Cyanoramphus unicolor*), and the Australian Rock Parrot (*Neophema petrophila*) (Forshaw 1973). Nesting in holes in vertical cliffs is a relatively common habit in the family and is known for some *Amazona* species (King et al. 1979). Most amazons, however, nest in tree cavities, as do all other subspecies of *Amazona leucocephala* (Bangs 1916, Barbour 1923, Noegel 1976). The only reference we have found to Inaguan parrot nests is that of Cory (1880), who reported Bahamians finding them in tree cavities. Similarly, all four nest sites we examined on Great Inagua in 1979 were in trees, as were all nests described to us by island residents. We have found no nesting records for other, extinct, populations of the Bahama Parrot.

The subterranean breeding on Abaco probably relates to several factors: a relative scarcity of good nest sites in trees, especially *Pinus caribaea;* an abundance of good ground sites; and the absence of native terrestrial mammalian predators. *Pinus caribaea* appears to be an extremely poor cavity-former, and except around Buzzard Hill, we found no hardwood coppice with trees large enough to provide cavities of adequate size. However, in a freshwater swamp region along the west coast of southern Abaco, we did find a few hollow *Sabal palmetto* (pond top palms) that were large enough inside to be usable. Parrot pairs were common in the region although the high water table precluded use of any holes in the ground. As the palms appeared to offer the only potential nest sites there, we inspected a fair number of stubs for signs of use. No sites were then active, but later that summer a local resident showed Clarke Carraway (pers. comm.) a parrot nest in a hollow *Sabal palmetto* in this region. Carraway was also told of other such sites. We suspect our failure to find active nests there in May might have been because egglaying had not yet begun in this particular area. On Abaco *Sabal palmetto* appears to be limited to a few swampy regions, and judging from interviews with Abaconians, we think underground nesting is usual for the species on this island.

The six parrot nests we located on Abaco were in regions with low water tables, and all were in spacious subterranean cavities (Table 3; Figures 5 and 6). One site found in November 1976 was inactive; the other five were active in May 1977. That the November 1976 site was a former parrot nest was clear from typical marks of parrot "chewing" on branches at the entrance of the hole; it was only about 100 m (328 ft) from one of the May 1977 sites and could have been an earlier nest of the same pair.

TABLE 3

Measurements of Bahama Parrot Nests

Nest no.	*Nest substrate*	*Ht. above ground (m)*	*Entrance (cm)*	*Depth (cm)*	*Bottom internal diameter (cm)*	*Comments*
Abaco:						
1	limestone rock	0.0	15 × 25, 15 × 25	147, 175	51-61 (estimate)	Two entrances, active 1977
2	"	0.0	23 × 25	157	30 (minimum)	Active 1977
3	"	0.0	25 × 41	244	41 (estimate)	Active 1977
4	"	0.0	23 × 30	152	38 (minimum)	Active 1977
5	"	0.0	8 × 28	107	30 (minimum)	Active 1977
6	"	0.0	15 × 30	213	61 × 61 (triangle)	Old nest 1976
Great Inagua:						
1	*Bucida buceras*	3.4	6 × 10	81	15 (estimate)	Active 1979
2	"	0.6	8 × 60	48	20 × 25	Active 1978
3	*Avicennia germinans*	2.1	14 × 16	102	17 × 23	Active 1978
4	*Guaiacum sanctum*	1.8	8 × 16	53	17 × 20	Active 1979

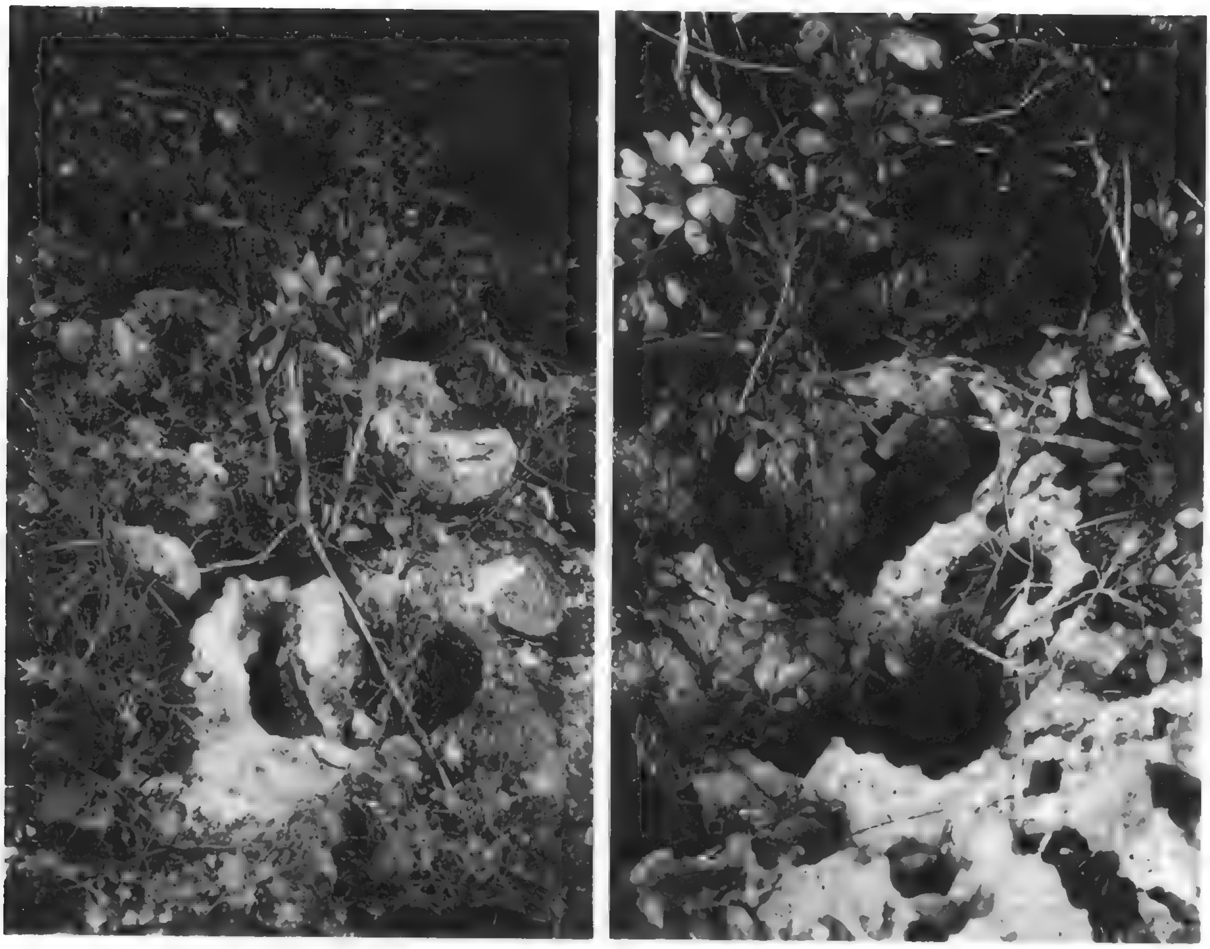

Figure 5. Two active parrot nests of 1977 on Abaco. Photos by N. F. R. Snyder.

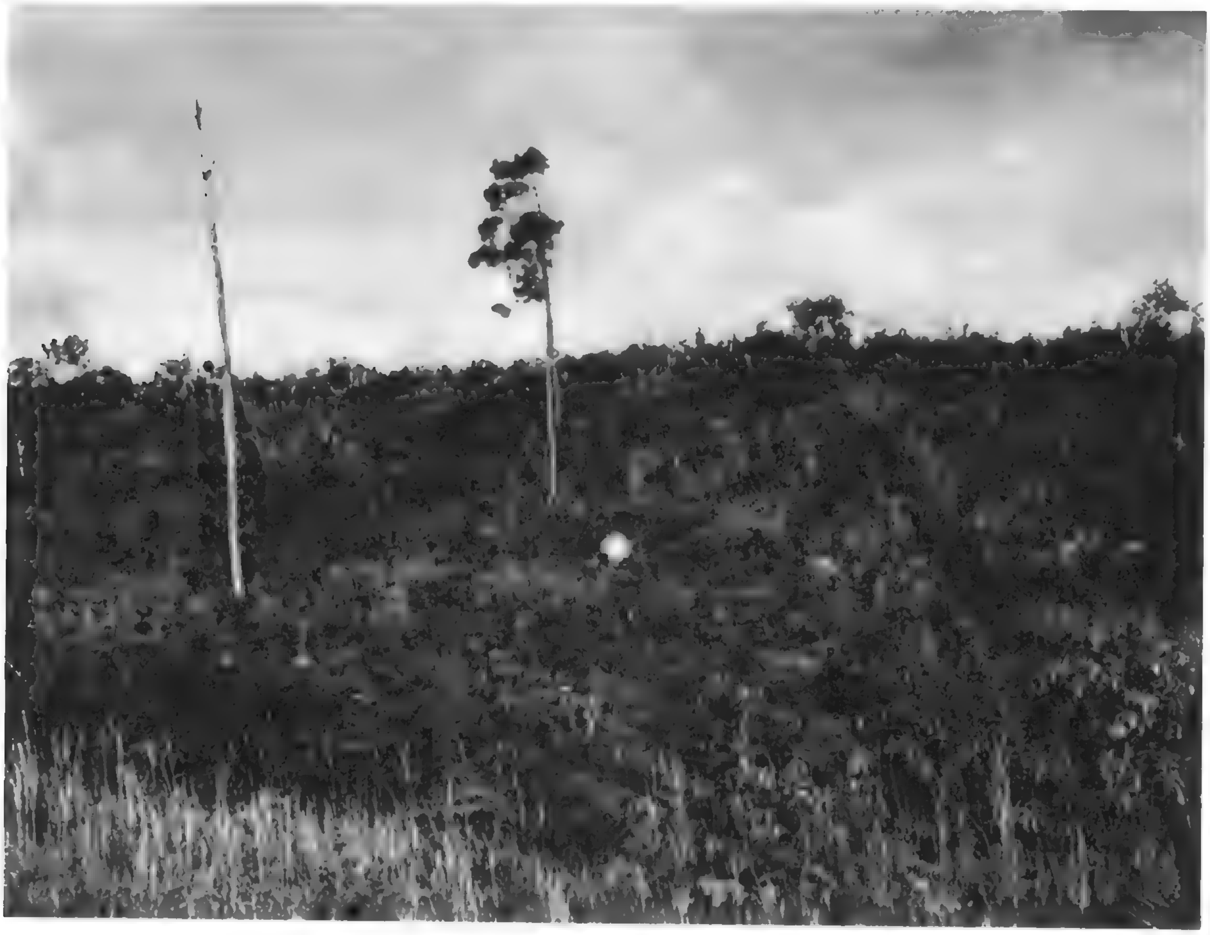

Figure 6. Inactive Bahama Parrot nest found in November 1976 (C. B. Kepler standing at the site). Photo by N. F. R. Snyder.

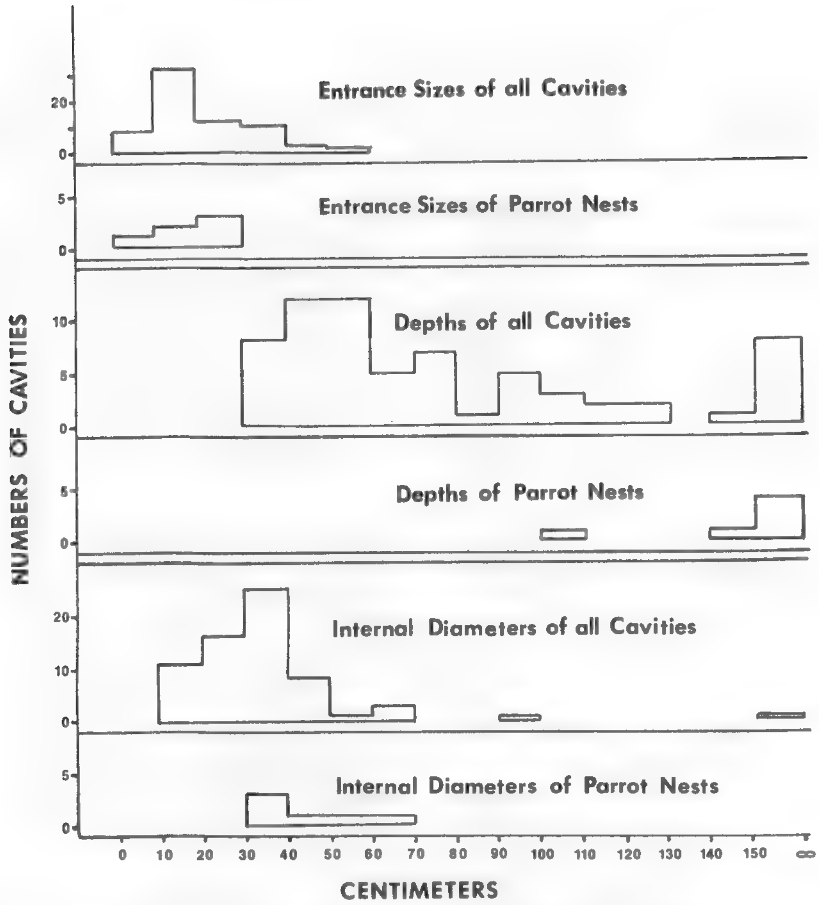

Figure 7. Histogram comparing depths, internal diameters at bottoms (minimum), and entrance widths (maximum) of Abaco parrot nests and nearby holes.

Figure 7 compares cavity dimensions of the Abaco parrot nest holes with dimensions of nearby unused holes. For the sample of nearby holes, we located 10 cavities adjacent to each nest by following a spiraling path outward from the nest until 10 cavities were encountered. We measured only holes with a miminum depth of 30 cm (12 in.) and with entrance widths between 6 and 61 cm (2.4 and 24 in.), and in all instances found them within a radius of about 30 m (100 ft) from the parrot nest.

The comparisons in Figure 7 indicate that parrots were occupying relatively deep sites with roomy bottoms. Five of the nests had overhangs or ledges within the cavities. In all nests with eggs, it was clear that the parrots were preferentially placing the eggs under these obstructions as best they could. Abaco residents who also had seen underground nests told us that parrots commonly nested under ledges within holes and that eggs and young were seldom visible from the nest entrances. It thus appears that the species prefers to conceal its eggs. Nest entrance sizes varied; the narrowest was crescentic, only 8 cm (3.2 in.) wide at its widest (Figure 5a).

In the nesting areas on Abaco, potential nesting holes were abundant yet parrots were exploiting very few of them. The active nests we found were well separated from each other: nests 1 and 2 were 400 m (1,312 ft) apart; nest 3 was 800 m from nest 2; and nests 4 and 5 were 166 m from each other. Although all nest holes were directly exposed to rainfall and presumably had been formed by ground water percolation, all appeared to be relatively dry at the bottom (as were most nearby holes), and the eggs were not visibly soiled by contact with the substrate. Like most psittacids, Bahama Parrots do not use nesting material, but simply deposit their eggs directly on the floor of the cavity.

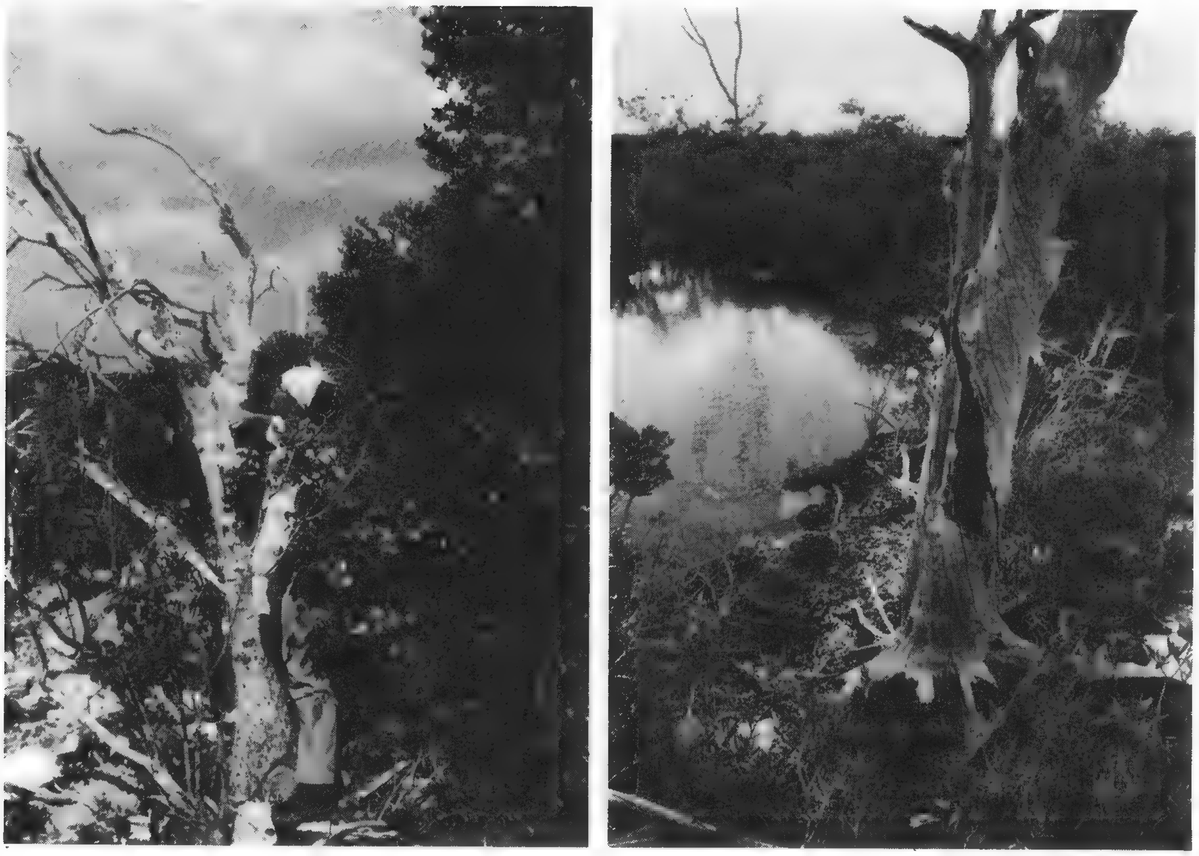

Figure 8. Two Bahama Parrot nests on Great Inagua: left, a site discovered in 1979 by H. Snyder; right, a site found by James Nixon in 1978. Photos by N. F. R. Snyder.

None of the residents we interviewed on Inagua had ever heard of parrots nesting in holes in the ground. However, one area (Devil's Point, just north of Matthew Town) has a few potholes similar in structure and quality to those seen on Abaco. Potential tree nest sites, although not abundant on Inagua, seemed more numerous than on Abaco. The four nests we examined were in Inagua oak (*Bucida buceras*), lignum vitae, and black mangrove (*Avicennia germinans*) (Table 3). In addition, James Nixon recalled having seen nests in poisonwood, coconut palms, mahogany (*Swietenia mahagoni*), and wild tamarind. The four nests we checked were all much smaller than those we found on Abaco and other *Amazona* nests we have studied in the West Indies. Our impressions were that Inagua parrots might be suffering from a scarcity of optimal sites. Internal diameters of the four nests were all less than 25 cm (10 in.), and they appeared to be tight squeezes for the birds (Figure 8). Moreover, in fairly extensive searching through the terrain surrounding the known nests, we found no tree cavities with larger internal dimensions and very few with holes approaching the sizes of the known nests.

Pre-egglaying Behavior

The behavior of the ground-nesting Abaco parrots early in the breeding cycle differed in several important respects from behavior of other West Indian *Amazona* species. The pairs we observed were only mildly territorial in the vicinity of their nests; we saw none of the vicious intraspecific battling reported by Snyder et al. (MS) for the Puerto Rican Parrot (*A. vittata*) and the Hispaniolan Parrot (*A. ventralis*). Only along the wet western side of southern Abaco, where there were no potential subterranean nest sites and only a moderate abundance of holes in dead palm stubs, did we record any vigorous territorial behavior. Because other *Amazona* parrots are strongly territorial throughout the breeding cycle, we do not believe the absence of intraspecific strife in the ground-nesting populations was a function of the stage of reproduction. Instead, we suspect it was related to the superabundance of good potential nest sites available to these populations—an usual situation.

Another difference concerns roosting behavior. Of the five ground-nesting pairs of Bahama Parrots we studied on Abaco, none roosted near the nest before (apparent) egglaying. This is unusual behavior for *Amazona* parrots and may also be related to the lack of competition for nest sites (and hence the necessity to guard them constantly). Until laying, the nesting pairs still associated with other parrots at distant communal roosts and only inspected their nests at irregular intervals during the day. As egglaying approached, the female (presumably) of each pair began to remain within the nest hole through most of the day while her mate foraged, but she still flew off each evening with him to the communal roost. At intervals during the day the male returned and called her from the nest for feedings, a pattern typical for *Amazona* parrots just before laying (Table 4).

We did not have an opportunity to make detailed observations of pre-egglaying behavior of the Inagua parrots, although our visit apparently coincided with this stage. Parrot pairs were in attendance at only two of the four nest sites we examined (the other two were inactive in 1979), and we watched the pair inspect a nest at only one site. This pair was nesting distant from other parrots so we did not observe any territorial interactions. The other active pair defended its nest tree from other parrots with vigorous vocalizations, but we saw no physical battles during our brief observations.

Copulation

We witnessed eight copulations by four different pairs on Abaco. All followed the pattern typical for New World parrots: the male stood beside his mate, gripped the perch with one foot and rested his other foot on the female's back while she swayed her tail back and forth against his tail in an irregular fashion (Smith 1973). The male fed the female before each of four closely-observed copulations. Twice the male clearly was on the female's right and twice he was on her left. The other observations were too distant to be sure of the relative orientation. Durations of several copulations were: 1–2 min, 95 sec, about 30 sec, 40 sec, and a minimum of 67 sec—closely similar to copulation durations of the Puerto Rican Parrot (Snyder et al. MS). Once a male was seen to fan one wing over the back of a female at the moment of cloacal contact, also a common but not invariable movement in the Puerto Rican species.

Timing of Egglaying

Of the five pairs studied closely on Abaco, two had not laid eggs before our departure on 28 May. The other three pairs had clutches of 3, 4, and 1 egg, respectively, on 27 May (the pair with the single egg had just begun laying). The three pairs with eggs were all located in a nesting area that was well separated from the two pairs that had not yet laid, which suggested local differences in timing of reproduction. Two of the pairs with

TABLE 4

Entries and Exits of Adult Bahama Parrots at Two Nests during the Egglaying-Incubation Period

Date	*Observation times*	*Observers*[1]	*f*[2] *exits*	*f enters*	*m*[2] *enters*	*m exits*	*Comments*[3]
Nest 2:							
20 May	0540–1345	J. G.	0610	0658			f exits with no preceding calls from m.
					0658	0703	m follows f into hole.
					0844	0915	m enters when f does not respond to calls; nest contains at least 1 egg.
22 May	0555–2025	N. S.			0636	0638	m enters when f does not respond to calls.
			0638	0656			f exits only after m enters.
					0756	0800	m enters when f does not respond to calls.
					0959	1006	no calling by m before he enters.
			1750	1818			f exits after m calls.
					1920	1929	m enters when f does not respond to calls.
24 May	1500–1830	R. W.	1805	1815			f exits after m calls.
25 May	0550–2030	M. S., W. K.	0854	0910			f exits after m calls.
			1758	1812			f exits with no (audible) preceding calls by m.
					1933	1938	m enters when f does not respond to calls.
26 May	1530–2010	N. S.	1809	1827			f exits after calls of m.
27 May	1500–1915	N. S.	1511	1525			f exits but m not in vicinity.
			1826	1855			f exits in response to calls of m; nest contains 4 eggs.
Nest 3:							
20 May	0600–0825	W. K., M. S.	0632	0803			f exits after m calls, possibly delayed in returning by observers' presence; nest contains 1 egg.
22 May	0615–1955	W. K., R. W., D. S.	0634	0758			f exits after m calls.
			1441	1518			f exits after m calls.
			1844	1945			f exits after m calls.
24 May	1745–1930	M. S.	1913	—			f exits after m calls; observer leaves.
26 May	1745–1920	M. S.	1840	—			f exits after m calls; observer checks nest contents (3 eggs) and f returns sometime after 1858.

[1] Observers' initials as in Table 1; also Deborah Shaw.

[2] f = female; m = male.

[3] Both pairs were actively laying during the period, so to avoid disturbance, nests were not checked daily.

eggs apparently began their clutches about 19 May; the third began about 26 May. Egglaying in late May and (presumably) early June is consistent with reports by Abaconians, who have found eggs in nests in May and young in June and July.

During our Inagua visit in late March 1979, the parrots were mostly assembled in flocks, and we saw signs of reproductive activity in only two pairs, neither of which had laid eggs. However, a nest found in 1977 by Ed Haxby apparently had eggs by about the middle of March 1978. This was a nest from which four young were taken into captivity in late May 1978. Now in a captive breeding program of Lynn Holowesko, the President of the Bahamas National Trust, these young fledged about the second week in June. If one allows 26–27 days for incubation and 9 weeks for nestling life (figures from the Puerto Rican Parrot), egglaying at this Inagua nest probably began about 15 March. The three young produced in one of the 1979 nests (Figure 8a) were also taken as stock for Holowesko's breeding project. These chicks were photographed at about 6 weeks of age on 8 July, hence eggs were probably laid about 1 May. Although these nests are few, their dates suggest a somewhat earlier breeding season on Inagua than on Abaco.

Compared with other West Indian amazons (Snyder et al. MS), egglaying in the Bahama Parrot, especially the Abaco population, is late. Most *Amazona* species lay eggs from January through March or early April, depending on elevation. To our knowledge, only one high elevation population of the Hispaniolan Parrot lays as late as the Abaco birds (J. W. Wiley pers. comm.); Hispaniolan Parrots at sea level generally lay in January.

Why the Bahama Parrot is delayed in breeding is not known. Its late season may reflect the comparatively cooler climate that far north, and consequently delayed fruiting seasons of important food plants. Whether or not breeding is timed to coincide with a particularly abundant food source must await answer from detailed studies of the parrot's food habits. Egglaying probably is not timed to minimize the risks of flooding of nest holes; rainfall on Abaco peaks in June at 23 cm (9 in.) and is lightest (monthly means about 8 cm or 3 in.) in January through April.

Incubation

At the three Abaco nests with eggs, one member of each pair (presumably the female, as in other *Amazona*) remained within the nest more or less constantly during egglaying and incubation, while her mate did virtually all the foraging. At two nests we made extended watches of entries and exits of the birds (Table 4). Males made three to five feeding trips to the nest vicinity per day. In most instances they did not enter the holes, but called their mates out with loud vocalizations from a nearby tree or shrub. Evidently females recognized their mates by voice alone because they did not exit in response to calls of other parrots. On leaving her nest, a female typically paused only momentarily on the lip before flying directly to a nearby tree, followed by her mate (Figure 9). Both birds usually called loudly during this flight. The male then fed his mate in the regurgitation fashion typical of *Amazona* parrots. They often copulated after feedings and shifted perches several times to call at distant pairs before the female returned to the nest. The male parrot usually returned with the female to the vicinity of the nest and perched for a few minutes in a tree or shrub before flying off again.

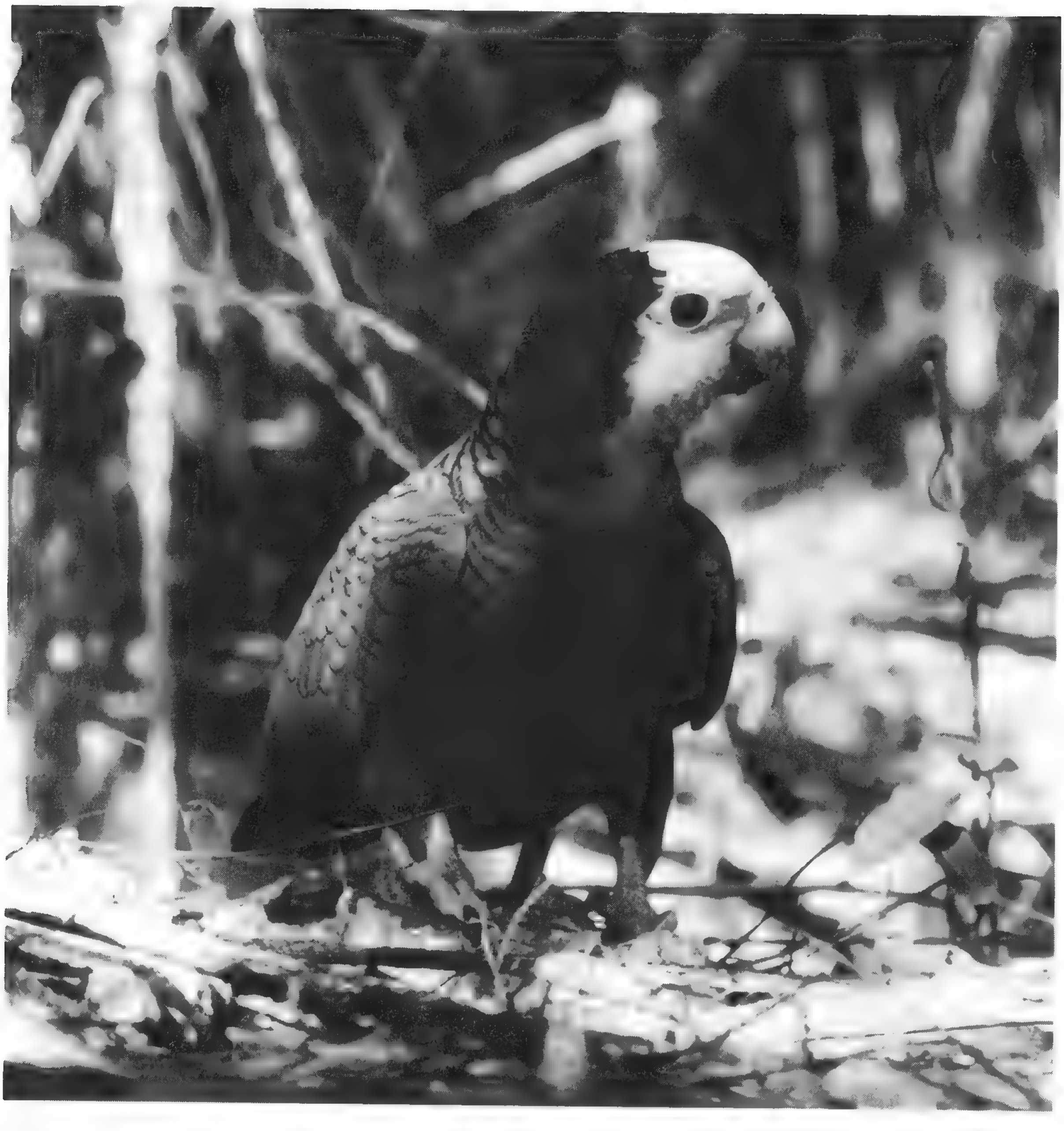

Figure 9. Female Bahama Parrot pausing momentarily on nest entrance before flying off to be fed by male. Entries and exits from nests were rapid. Photo by N. F. R. Snyder.

One male entered his nest several times during the day, apparently to feed the female. These entries generally followed what appeared to be unsuccessful attempts to call his mate out of the hole. Usually his mate left the nest only once in the morning and once in the evening. At the other closely-observed nest we never saw the male enter the hole, and at neither nest did the male roost in the nest hole overnight.

Although the behavior of the adults around nests was generally similar to what has been recorded for the Puerto Rican Parrot (Snyder et al. MS), there are a number of differences: (1) Bahama Parrots do not loiter on the lip of the nest; (2) the males regularly vocalize loudly when summoning mates from nests; and (3) both sexes frequently vocalize loudly as the female flies from the nest to be fed by the male. In general, Puerto Rican Parrots are far more secretive near their nests than are the Abaco birds. Puerto Rican pairs that are not harrassed by other parrots are sometimes almost completely silent around the nest. This difference could relate to greater predation pressure in Puerto Rico than in Abaco, although we have no direct data on predation rates for the Abaco birds to substantiate this hypothesis.

The speed with which Bahama Parrots entered and left their nest holes suggested to us that they were uneasy on the ground, and we did not see them on the ground at any other times. *Amazona* parrots in general are strictly arboreal; in many years of study in Puerto Rico, for example, parrots were seen on the ground only occasionally, at the end of first fledging flights or during territorial battles.

Nestlings and Fledglings

We could not return to Abaco in mid-summer to study nesting success and the birds' behavior in the late breeding season. Presumably the incubation period of this species is similar to that of other *Amazona* of the Greater Antilles, i.e. about 26–27 days. Because the females of at least two and probably all three pairs studied covered their eggs soon after the first was laid, hatching is probably asynchronous, as in other *Amazona*. Nestling periods in the Puerto Rican Parrot average about two months, so Bahama Parrots on Abaco may fledge in late August. In November 1976 we sometimes heard begging calls of juveniles in parrot flocks and concluded that fledglings probably associate with their parents for a few months after leaving the nest.

THREATS TO THE ABACO POPULATION

Abaco parrots have faced threats of varying intensity over the years. The major real and potential problems appear to be: (1) accelerated change and destruction of habitat by man, (2) shooting, (3) taking of pets, (4) predation by feral mammals, and (5) hurricanes.

Habitat Alteration

Road construction and associated destruction of pines in the 1950's and 1960's were major intrusions into the primary habitat of Abaco parrots. It is unlikely that extensive mature pine forests will ever return to the island because the Bahamian government has plans to cut regenerating pines in approximately a 20-year rotation. Although this logging schedule will be possible in the northern part of Abaco, in the southern region of the island, extensive fires (reputedly started by pig hunters seeking to drive their game toward roads for convenient shooting) have recently become exceedingly frequent (Henry 1974). For example, between November 1976 and May 1977 a region of about 25–35 km^2 (10–13 mi^2) had burned in the central part of the southern third of Abaco; and during our May trip we saw evidence of several other recent burns and three more fires in progress. Except for those that directly threaten settlements, fires are not fought; they are simply allowed to die out. Although the pines are adapted to withstand periodic burning, the recent frequency of fires over large areas has undoubtedly exceeded the tolerances of the trees—they have no chance to regenerate.

To what extent the fires and continued suppression of pines in southern Abaco are harming the parrots is a difficult question to resolve. The species clearly does not require pine, *per se*—witness the former presence of parrots on many of the pineless southern Bahama islands—and we found the parrots foraging extensively in the hardwood scrub that has replaced the pines in many parts of Abaco. Charred stumps indicated that both of the major nesting areas we studied had been burned within the previous five to ten years. Although the parrots in these areas are now nesting in essentially open landscapes of low scrub (Figure 6), where presumably they had historically nested in mature pine forests, we are not certain to what extent this change may have been to the parrots' detriment; subterranean rock nest sites are not destroyed by fire or lumbering. On the other hand, a terrain that is largely charred rubble without any sort of fruit-bearing vegetation cannot support a parrot population. With the increasing frequency of man-caused fires, most of the former pine yards could be burned simultaneously, leaving the parrots no food supply at all. We found no parrots in recently burned areas on the island, and at both of the major nesting areas we located, parrots did have some nearby living pines in which to forage. Moreover, they were feeding heavily on pine during the early breeding season. This feeding may not represent a dependency on pine at this time of year, but we might not have found parrots nesting in other areas because they did not have nearby pines.

Hunting

Elderly residents of Sandy Point told us that years ago parrots sometimes assembled to roost in mangroves near town. When the birds appeared, the townspeople ran out to shoot into the flock, killing numbers at a time. One lady remembered flocks as large as 100 or more birds. She also remembered that parrots tasted very good and were regularly eaten. She recalled that she last saw flocks in 1932—the year that area's pines were first cut (Henry 1974). In the 1930's roads had not yet been built into the island's interior and it is unlikely that the Sandy Point shooting had a major impact on the population as a whole. The disappearance of parrots from Sandy Point may have been more a result of logging than of hunting.

According to John Roberts, shooting became common in the interior of Abaco only after construction of the road system allowed easy access. Reportedly, many parrots were shot in the 1960's in hopes of only wounding them so they could be taken as pets. This practice apparently has declined as awareness of the Bahamian laws protecting parrots has increased. We saw abundant evidence (spent shells and feather piles) of recent hunting of White-crowned Pigeons (*Columba leucocephala,* a legal game species) in southern Abaco, but we found no parrot feathers mixed with those of the pigeons, even in locations with many parrots nearby. The $500 fine seems to be acting as an effective deterrent. Every resident we interviewed was aware of the fine, and we heard of no recent hunting of parrots.

Parrots are easily shot because they are noisy, slow-flying, and gregarious. Moreover they often fail to disperse when shot at; instead they remain within range, apparently attracted by the distress calls of fallen flockmates. Shooting has been an important cause of decline for most endangered West Indian psittacids (Forshaw 1973). With the extensive road system now in place in southern Abaco, renewed hunting could quickly decimate the parrot population.

The Pet Trade

The first trade items that Columbus received from New World natives were captive Bahama Parrots (Morison 1963); clearly the taking of parrots for pets long preceded the European invasion of the West Indies. How the modern pet trade has affected parrots from the Bahamas is unknown, although Allen (1905) reported that young of the now-extirpated population on Acklins Island were "regularly" taken as fledglings and transported to the Nassau market for sale. Apparently the Abaco parrots have not been affected by the pet trade to the same extent as have other *Amazona* species in the West Indies. The illicit capture of birds for pets has been a major factor in the decline of the Puerto Rican Parrot and several species of Lesser Antillean parrots that now are close to extinction. Although we heard that some Abaco nestlings are occasionally taken illegally (mostly for local sale in Marsh Harbour), no major industry has yet arisen and one can only hope that it never will. Here, too, the protective Bahamian laws seem to be effective.

Feral Mammals

Feral cats are abundant on Abaco, and we usually saw at least one or two daily during our visits. To what extent they prey on parrots and their nests is unknown, but we strongly suspect that predation does occur. The wild cats of Abaco probably subsist largely on the abundant small lizards, but we doubt that they would pass up a chance at a parrot nest. We have no information on when feral cats became established on Abaco. The first (unsuccessful) European colonization of the island was in 1625, and after many decades of casual visitation by pirates and other seafarers, Abaco was permanently settled by Loyalist refugees from New York and New England in 1784 (Durrell 1972). Thus cats may have been introduced to the island more than 300 years ago, and almost certainly have been present for the past two centuries. If cats were an overwhelming threat, the parrots would likely have been wiped out long ago.

Fortunately, the mongoose (*Herpestes auropunctatus*) has never been introduced in the Bahamas. This voracious predator has not threatened tree-nesting parrots elsewhere in the West Indies, but the ground-nesting Abaco birds probably would have no defenses against it. Although the mongoose was introduced into the West Indies primarily late in the 19th century, the recent discovery of this predator on Dodge Island near Miami, Florida (Larry Thomas pers. comm.), and the recent mongoose invasion of Kauai in the Hawaiian Islands (John Sincock pers. comm.), give warning of the continuing threat this creature represents to ground-nesting birds on tropical islands.

The vulnerability of ground-nesting birds to introduced terrestrial predators is well illustrated by the present difficulties of the New Zealand Kakapo. This parrot has been driven to near extinction by introduced stoats (*Mustela erminea*), and until some Kakapos were discovered on stoat-free Stewart Island in 1976, all attempts to find females in the dwindling population on South Island had been fruitless (Merton 1975, and pers. comm.).

When we examined occupied nests of Abaco parrots, we saw none of the frantic nest defense characteristic of Puerto Rican and Hispaniolan parrots (Snyder et al. MS). The sitting birds were completely silent and still and made no attempts to attack our tape measure when we lowered it in the cavities. Their apparent passivity could reflect the lack of significant terrestrial predators in their evolutionary history. Alternatively, "freezing" may be the best defense for an underground parrot faced with a feral cat or a human. Cats are known to abandon potential prey that does not move, and a human without a flashlight would find it difficult to determine whether an underground cavity was an occupied parrot nest unless the bird made a noise or moved.

Hurricanes

Hurricane Betsy in 1965 had a massive effect on southern Abaco. Henry (1974) described the impact of the storm in some detail, and there can be little doubt that many parrots were lost. Thompson (*in* Henry 1974) reported finding *no* bird life after the storm in the region between Sandy Point and Crossing Rocks. The major impact of hurricanes on land birds appears to be starvation caused by destruction of food supplies, although undoubtedly many birds are also lost through physical battering. The logging of southern Abaco permitted intensified damage by the storm. The exposed seed trees were no match for the winds, and the result was a long-term destruction of the pine forests. Hurricanes, although not a frequent stress, are sometimes extremely important for species reduced to small isolated populations, lacking refugia from which devastated areas can be repopulated. The effect of hurricanes in recent extinctions in the West Indies has been discussed by Raffaele (1977).

CONSERVATION OF THE BAHAMA PARROT

Abaco

The periodic cutting of the Abaco pine yards will probably continue. This lumbering may not threaten the survival of parrots if adequate refugia are left in the pine and coppice zones and if the frequency of fires can be controlled. However, most of the coppice is privately owned and there have been, and surely will continue to be, attempts to develop this land for vacation homes and resorts. The pine yards are government-owned so they might be more easily managed to allow parrot survival. Too little is presently known about the parrots' biology to design a comprehensive long-range management plan. Until such a plan is possible, however, certain initial steps would be beneficial to undertake. Parrot refuges — selected areas with abundant nest sites and good food supplies — could be established. Management of these refuges should include road closures that would result in reduced incidence, if not complete exclusion, of fire, and in the eventual regeneration of the pines. Later, the regenerated pine yards could be logged on a staggered schedule to ensure continuous availability of large pines to the parrots while also allowing for sustained pulpwood production.

Inagua

All indications suggest that the Inagua population of the Bahama Parrot is in good health. Unlike the Abaco birds, the parrots of Inagua are exceedingly tame, often allowing approach to within 3 m—a characteristic that probably reflects a relatively low level of human persecution in the past. Residents of Inagua, like those of Abaco, are well aware that the parrot is protected, and according to the Nixon brothers, shooting of the birds is now rare. Without pines or other valuable natural resources to develop in the interior scrub forests of the island, there has been no impetus for building an extensive road system, a situation not likely to change in the near future. And without roads, the degree of contact between parrots and humans will likely remain small, perhaps the most important security factor for the birds. Hogs are hunted on the island, but fires are seldom set to drive game. The few Inaguans who still farm have some animosity toward parrots (as crop pests), but it seems doubtful that local agriculture will expand in the near future to form a serious threat to the birds. Adding considerable security to the situation is the large refuge area currently controlled by the Bahamas National Trust.

Another potential threat is nest predation and competition by Pearly-eyed Thrashers (*Margarops fuscatus*)—a major cause of nesting failure for the Puerto Rican Parrot in recent years. This hole-nesting thrasher occurs on Great Inagua (not on Abaco) but is uncommon, and we saw no evidence that it has been giving the Bahama Parrot any difficulties. We found no thrashers in the areas where we saw parrots, and according to Alexander Sprunt, *Margarops* is largely limited to the northwestern part of the island where it is not especially abundant. None of the Inaguans we interviewed had seen or heard of interactions between thrashers and parrots, but the potential for serious competition exists wherever nest holes are in short supply.

Reestablishment on Other Bahama Islands

With a maximum population probably not exceeding a few thousand individuals and a history of steadily declining range and abundance, the Bahama Parrot cannot be considered secure. An attempt to reexpand the range of the species might greatly increase its safety from catastrophes—both man-caused, and natural threats like hurricanes. The Bahama Parrot could be reestablished on other islands in the archipelago, provided adequate protection from human depredation could be assured. Reintroduction on Acklins Island now seems particularly feasible, given the bird's recent occurrence there, the island's comparative stability of habitat (M. H. Clench pers. comm.), and the general present-day respect of Bahamians toward bird protection laws. In some respects, the Abaco population of parrots, with its flexibility in nest-site tolerances, would seem a logical source from which to create new populations; but the Inagua population is larger and can better afford to be the donor. We do not advocate large-scale withdrawals of parrots from either source until the success of introductions is proved, nor do we advocate attempts to introduce the species into areas outside its historic range, but we do urge the eventual restocking of the species to many of the islands on which it once occurred and from which it probably was extirpated by man.

CONCLUSIONS

Especially in view of the extraordinary nesting habits of the Abaco population, the Bahama Parrot represents a unique wildlife resource worthy of preservation. The Bahamian Government has already demonstrated a commendable concern for the parrot's protection, and we hope that further steps can be taken to ensure its survival. Of primary importance for the conservation of the species will be future efforts to: (1) monitor the size of both the Abaco and the Great Inagua populations, (2) establish reserves for the species on Abaco, (3) study the impacts of burning and lumbering on Abaco, and (4) reestablish the species in parts of its former range elsewhere in the Bahamas.

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We are particularly indebted to Angela Kepler for preparing the figures, and to Mats and Ylva Segnestam, Jesse Grantham, Angela Kepler, Rick Warner, Deborah Shaw, and Helen Snyder, who were part of one or another of the field parties and who contributed much more than assistance in the field.

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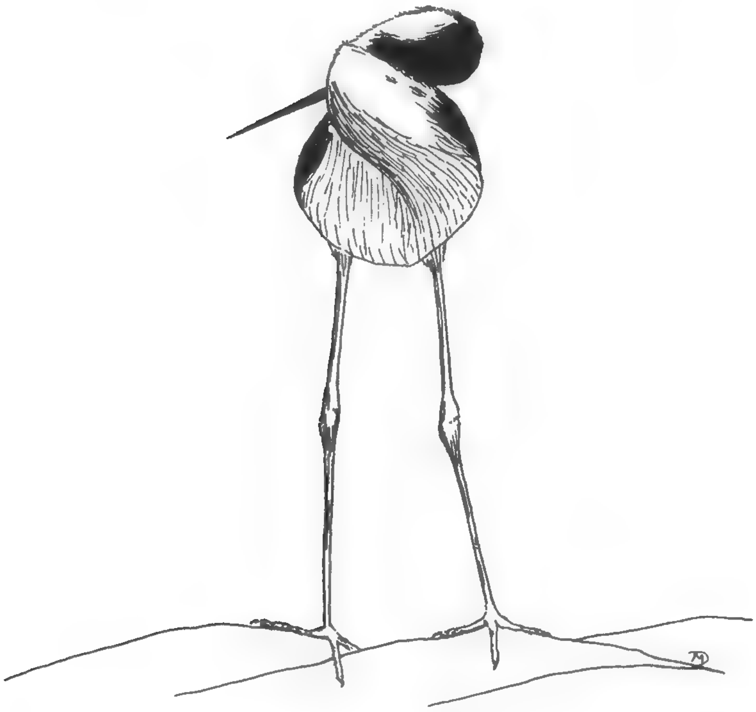
UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
PATUXENT WILDLIFE RESEARCH CENTER
CALIFORNIA FIELD STATION
87 N. CHESTNUT STREET
VENTURA, CALIFORNIA 93001

871 DOLLY MADISON BOULEVARD
McLEAN, VIRGINIA 22101

and

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
PATUXENT WILDLIFE RESEARCH CENTER
HALEAKALA FIELD STATION
248 KAWEO PLACE
KULA, MAUI, HAWAII 96790



Black-necked Stilt, *Himantopus mexicanus.* Drawing by David S. Maehr.

LLOYD
SANDFORD

NOTES ON THE PLUMAGES OF THE BOAT-BILLED HERON

ROBERT W. DICKERMAN, KENNETH C. PARKES, AND JOSEPH BELL

Understanding the sequence of molts and plumages of a species permits one to better determine the age of individuals—information that is vital to documenting population structure, to species management, and in some cases, to clarifying species relationships. Fully understanding plumages and molts should also lead to more reliable field identification of "odd" plumaged individuals not often pictured in field guides.

Although the plumages of the Boat-billed Heron, *Cochlearius cochlearius,* undergo complex and often subtle changes from the natal plumage at hatching to the third basic, or definitive "adult," plumage at approximately two years of age, these plumages have persistently been described as only two—the "adult" and "immature" (or, erroneously, "juvenal") (Carpenter 1971, Griscom 1926, Haverschmidt 1969, Juarez and Dickerman 1972, Wetmore 1965). Dickey and van Rossem (1938) did note that the sequence of plumages of the Boat-billed Heron was similar to the three plumage stages of the Black-crowned Night-heron (*Nycticorax nycticorax*), but some later authors (e.g. Haverschmidt 1969) have not recognized a "subadult" plumage in *Cochlearius.*

Recently-collected specimens from Mexican and Central American populations of Boat-billed Herons, acquired during studies of their nesting development (Juarez and Dickerman 1972), taxonomy (Dickerman 1973), and feeding behavior (Biderman and Dickerman 1978), and specimens available in collections, now permit a more detailed analysis and description of the complex molts and plumages of the Middle American birds. We describe here, for the first time, the six plumage stages of the Boat-billed Heron, from hatching to the "adult," or definitive, plumage. We also add information on the colors of the soft parts (the bare skin about the face, the mouth lining, and the tarsi and toes). Some data are still missing on both the plumages and soft-part colors because nesting seasons vary from region to region, depending on local water levels and food supply, and because samples are still not available from any single population throughout the year.

We have been aided in this study by examining birds hatched and raised in the breeding colony at the New York Zoological Park. The birds are mostly derived from Central American stock (north of Costa

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Plate 1. Boat-billed Herons, *Cochlearius cochlearius,* painted at the New York Zoological Park by Lloyd Sandford. 1a (upper left): No. 1211R, a heron at 128 days of age in first basic plumage. 1b (upper right): No. 1145L at 15 months of age in first alternate plumage, beginning second prebasic molt. 1c (lower left): No. 1145L at 25 months of age in second alternate plumage with retained brown feathers of first basic plumage. 1d (lower right): No. 1145L at 4 years, 2 months of age in definitive alternate plumage.

Rica). The late Lloyd Sandford, artist for the New York Zoological Society, painted a series of pictures of Boat-billed Herons from this colony; four are reproduced here. Plate 1a shows a bird (1211R, hatched on 9 July 1967) painted on 13 November 1967 in first basic plumage. Plate 1b–d is of another bird (1145L, hatched 13 August 1966) painted in three different plumages, from first alternate to definitive alternate, on 21 November 1967, 17 September 1968, and 20 October 1970. The latter bird was also painted in "1969" (not shown here).

Our conclusions based on preserved specimens have been supported by examination of the living collection, although molts in captive birds are less regular and feathers of one plumage tend to be retained into a later stage.

SOFT-PART COLORS

The colors of the soft parts of recently hatched nestling Boat-billed Herons have been described (Haverschmidt 1969), as have those of birds in definitive plumage during the nonbreeding season (many authors); only Wetmore (1965) mentioned some of the soft-part colors of nesting adults.

When the birds hatch, the loreal and gular areas, the mouth lining, and the tarsi and toes are nearly uniformly yellow-green. As the birds age, these areas darken, losing the yellow cast; the front of the tarsi and top of the toes, and the lores and mouth lining become grayer. The most dramatic changes are in adults just before nesting; annually the mouth lining, lores, and gular area blacken. Adults taken soon after a definitive prebasic molt have grayish lores and dull, pale buffy yellow or dull olive gular areas. A few small black spots may be present in the gular area. It is apparent from specimens that as birds develop enlarged gonads, melanin suffuses the rest of the gular skin, turning it first dark gray, then black. Thus birds taken early in the breeding period may be immediately identified in museum series by their black gular pouches. We do not know how or when the black coloration is lost. Douglas Mock (in litt.) wrote that he was sure he had seen pale-throated birds rearing chicks.

PLUMAGES

Natal Plumage

The natal down and juvenal plumage have been previously illustrated in photographs or described (Bell 1966, Dickerman and Juarez 1971, Juarez and Dickerman 1972, Wetmore 1965).

The hatching plumage of *Cochlearius* is unique among herons in that it is sharply tricolored. Chicks recently hatched have sooty gray crowns that contrast sharply with their pearl-gray cheeks and back and their white venter. Further, the down of the crown is short, rather than long and hair-like as in most other herons.

Juvenal Plumage

Bell (1966) published photographs of nestlings, and Juarez and Dickerman (1972) described and illustrated the development of the juvenal plumage. They described this plumage based on three banded young that were 52, 40, and 40 days of age (p. 467):

> "The forehead, malar area, auriculars and sides are rich medium brown, darker in the subloral area. The crown is black, with the feathers of the nape elongated to 45 mm. The interscapular area and the lesser and middle wing coverts are rich brown, with some individuals showing a vinaceous [reddish wine-colored] cast. Remiges, rectrices, and rump area medium gray. The greater wing coverts are medium gray, edged with the brown of the interscapular area. The outermost primary and the feathers of the alula are paler than the other remiges and are tipped and edged with buff. All remiges and rectrices are still sheathed at 52 days.
>
> Ventrally the overall appearance is pale grayish brown to buffy brown, paling to whitish on the belly. The breast is nearly uniform but feathers may be lightly mottled or, especially medially, tipped with dusky gray. The flank feathers are weakly streaked. They have a medial white area, varying in width between individuals from 1.5 to 3.5 mm, that is bordered by medium gray streaks; and the feathers are edged with buffy brown."

Carpenter (1971), in studying the nesting colony at the New York Zoological Park, did not distinguish between the juvenal and first basic (his "immature") plumages.

First Basic Plumage

The first basic plumage of Boat-billed Herons has been misidentified by some authors as the "juvenal plumage." It is produced by the first prebasic ("postjuvenal") molt, which in Central American populations involves the entire body and begins before the rectrices and remiges are fully grown (by day 52 at least in one specimen at hand). In South American populations the first prebasic molt is apparently more complete, involving at least the inner primaries (1 through 6 or 7) and one or more pairs of rectrices.

The first basic plumage is generally similar to the preceding juvenal plumage except for a more compact feather structure and slight differences in color (Plate 1a). Salvin and Godman (1901) described (in Latin) a specimen from Atoyac, Mexico, that they called a "juvenile" but that was in the first basic plumage. The back is less richly reddish brown (more grayish) than in the juvenal, the forehead is grayish brown, and the black crown is only slightly crested, and when fresh has a powdery grayish cast. Elongated plumes never occur in this plumage stage. The underparts are pale ashy gray with a slight vinaceous wash (as if they had been dipped in weak red wine), and the flank feathers are centrally streaked with white. The undertail coverts are white-to-pale vinaceous, with white bases.

First Alternate Plumage

The first prealternate molt is incomplete and produces little noticeable change (Plate 1b). Somewhat larger and pointed posterior crown feathers, and a few fresh brown interscapular feathers are gained. Some tertials and inner secondaries may be involved in this molt, or more likely, new feathers found at this stage represent the earliest phase of the second prebasic molt.

Second Basic or "Subadult" Plumage

This plumage is gained by a complete molt toward the end of the first year. The breast, belly, thighs, and undertail coverts are more richly vinaceous than in the first basic plumage. The flanks become dull black. The rectrices and remiges gained are medium-to-dark gray and the back becomes more grayish brown (less reddish). The new underwing coverts are more strongly patterned with buff along the midvane, bordered by gray-to-black edges; in some individuals they are nearly black. The crown is deep black with only a moderate crest. Carpenter (1971) termed this the "pre-adult" plumage.

Second Alternate Plumage

A fresh, grayer interscapular area and broad elongate plumes are acquired by at least some individuals at this partial prealternate molt (Plate 1c). Like the first prealternate molt, the second may involve tertials and an occasional secondary. Two males with elongated plumes had testes measuring 5 × 11 and 9 × 20 mm, respectively, and a female had an enlarged oviduct and ovary (ova to 11 mm). As recorded from the fresh specimen of the male with larger testes, the gular area was dark gray and the interior of the mouth was gray with flesh-colored and purplish casts. The dried gular area of the female is near black (color when fresh not noted on label). The "adult" plumage of earlier authors is not this second alternate, but the definitive alternate plumage (terminology of Humphrey and Parkes 1959) as described beyond. Birds may be physiologically "adult" — as in the case of the above-described Boat-billed Herons in the second alternate plumage—before acquiring the definitive or "adult" plumage; thus the term "adult plumage" is meaningless in this species.

Third Basic, or Definitive, Plumage

Salvin and Godman (1901) described an "adult" male from Motombo, Nicaragua (translation from the Latin by John Farrand):

> "Above clear ashy, with the remiges and rectrices pearly-ash, on the primaries clearer; with the crown strongly crested [and] black; with the forehead ashy-white; on the sides of the face grayish-vinaceous; chin bare, but throat whitish; with foreneck and upper breast pale vinaceous chestnut; with sides of body, axillaries and inner underwing coverts black; with outer underwing coverts and [undersides of] remiges pale ashy; margin of wing white; with bill black; with feet soft [pale] green; with irides black."

With the large series of specimens now available, this description can be amended somewhat. Salvin and Godman described the female as darker, but based their description on a specimen of the sooty-colored race *C. c. panamensis.* In the Central American and Mexican populations, the mantle in the definitive basic plumage ranges from dark to pale gray with the majority being pale (Plate 1d). The average male is paler in color than the average female, but individuals of one series are interchangeable with those in the other; one female examined is among the palest of all individuals, and a male is among the darker specimens. Thus, although casual or careless observers (see Griscom 1926) have noted "pairs" with one member (presumably the female) darker in color, this is not consistent. During Mock's (1975) detailed behavior study, he was not able to use color to distinguish the sex of nesting birds.

In the few molting "adult" specimens at hand, the new feathers of a medium gray bird are also medium gray, and the new feathers of a molting pale gray bird are also pale. Interestingly, in Sandford's paintings of Boat-billed Heron 1145L, the first definitive plumage painted in "1969" is darker than a later definitive plumage painted in October 1970 (Plate 1d). Haverschmidt (1969), who was familiar with the nearly white South American populations (*C. c. cochlearius*), was in error when he noted that the "adult" in the color plate by Eckelberry (1965) was not fully adult because the back was too dark. Eckelberry's bird can be matched by darker birds in the series from Central America. True, the breast and flanks are too ruddy and dark, but this appears to be a problem of color reproduction.

Forehead color may, without geographic correlation that we can discern, vary from near white to creamy buff or pale grayish brown.

The exuberant crest of broad plumes is gained in a prealternate molt, up to six months before the herons nest. Males have longer plumes than do females. Crest plumes of seven birds with black gulars (but sex not known) in the New York Zoological Park measured 167 to 245 mm (6.6 to 9.6 in.) in length. The plumes are dropped during nesting, probably during the incubation period. Bell (1966) published photographs of incubating birds with long crests and of plumeless adults with half-grown young. Incidentally, Dickerman found an accumulation of the similar elongated head plumes of Chestnut-bellied Herons (*Agamia agami*) under the nests of incubating birds in Mexico.

WEIGHTS

So few weights are available for Boat-billed Herons from Middle America that we have combined data from diverse populations. Four males in first basic plumage weighed 514–625 g (18–22 oz; mean, 562 g or 20 oz); one female weighed 535 g. Birds in fully definitive plumage are considerably heavier—eight males weighed 685–770 g (mean, 716 g) and four females weighed 525–726 g (mean, 649 g). Thus the nocturnal Boat-billed Heron is smaller than the Black-crowned Night-heron, of which a male and two females in "first nuptial" (? first alternate) plumage weighed 845, 833, and 862 g, respectively, and two males and two females in "adult" plumage weighed 1,007, 1,014, 727, and 884 g, respectively (Gross 1923). Boat-billed Herons are about the same size as Yellow-crowned Night-herons (*N. violacea*); single specimens (age and sex not specified) of the latter weighed 652 and 660 g (Palmer 1962, Smith 1966).

DISCUSSION

The sequence of plumages of the Black-crowned Night-heron is probably similar to that of the Boat-billed Heron. Although a first basic plumage has not yet been described for the Black-crowned Night-heron, it occurs in the Rufous Night-heron (*N. caledonicus*), which Dickerman considers to be conspecific with the Black-crowned Night-heron. The subtle first plumage change of the Rufous Night-heron could easily have been missed were young birds not being handled frequently.

This study was greatly facilitated by our opportunity to observe the development of individual birds in the nesting colony at the New York Zoological Park. Unfortunately for many lesser known, although common, species, such an opportunity does not exist. For example, the molts and plumages of both the Black-crowned and Yellow-crowned night-herons have not been fully described. We hope that someone with access to breeding colonies of these North American species will soon fill these gaps in our knowledge.

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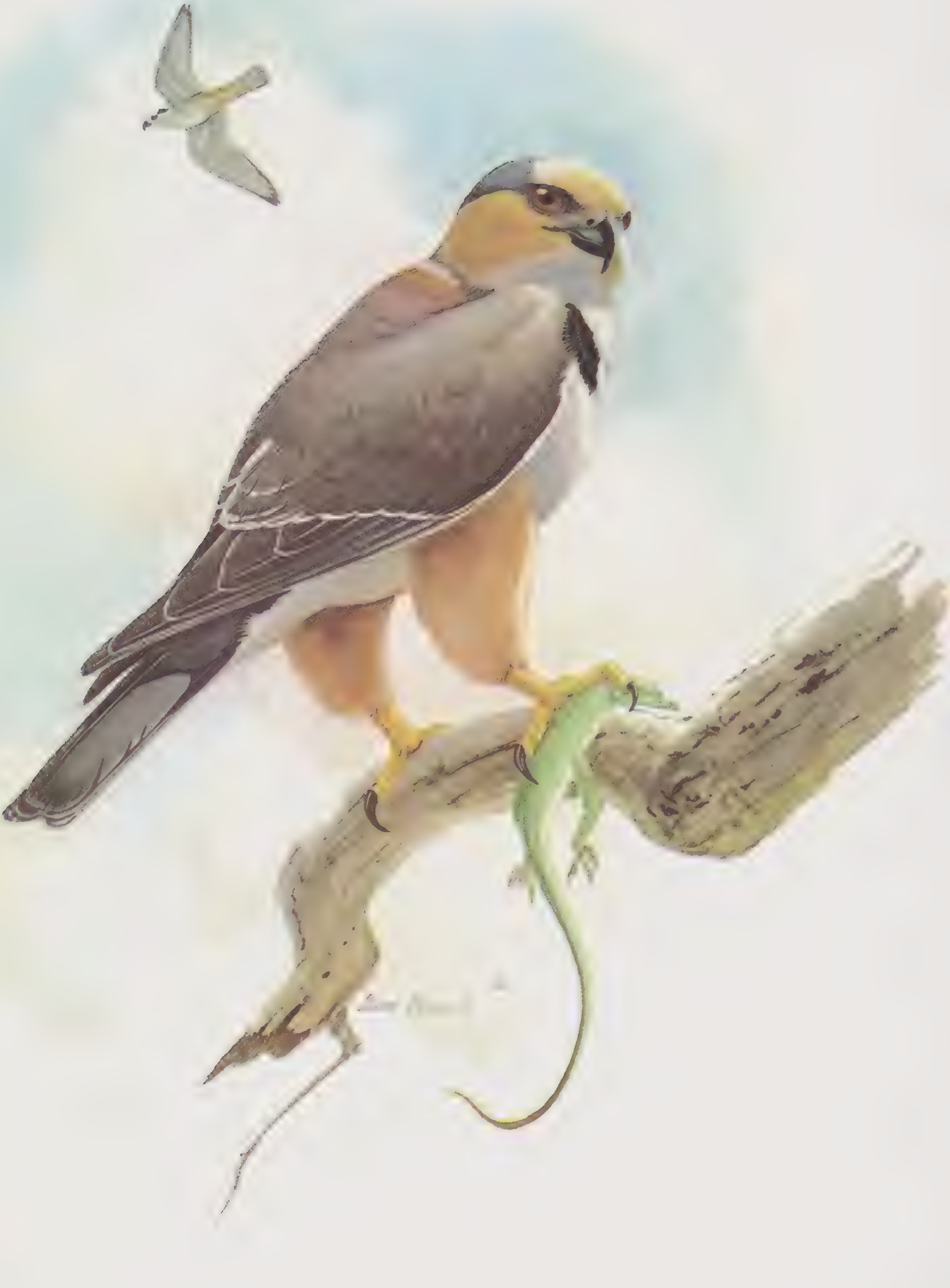
CORNELL UNIVERSITY MEDICAL COLLEGE
NEW YORK, NEW YORK 10021

CARNEGIE MUSEUM OF NATURAL HISTORY
PITTSBURGH, PENNSYLVANIA 15213

and

NEW YORK ZOOLOGICAL PARK
BRONX, NEW YORK 10406

Great Blue Heron, *Ardea herodias*. Drawing by Patrick J. Lynch, courtesy of the artist.



THE BREEDING OF THE PEARL KITE IN TRINIDAD

RICHARD P. FFRENCH

One of the smallest neotropical raptors, the Pearl Kite (*Gampsonyx swainsonii*) ranges over a wide area of South America from eastern Colombia, Venezuela, and the Guianas, south to Bolivia, Paraguay, and northern Argentina; isolated populations also exist west of the Andes from Colombia to Peru, and in Nicaragua (Brown and Amadon 1968; Blake 1977). Panama records are becoming more numerous, and perhaps the isolated population in a dry area of Nicaragua may eventually be joined with those to the south (D. Amadon pers. comm.). The Pearl Kite is a bird of open tropical woodlands and savannah and, like its relative the White-tailed Kite (*Elanus leucurus*), may be profiting by deforestation in Latin America. It is a rare resident in Trinidad.

Pearl Kites are diminutive members of the Accipitridae (kites, hawks, and eagles). The sexes are alike, but as with most raptors, the females are larger than males. They are basically slaty gray and white, although the gray becomes brownish with wear and fading; they also have a rufous-edged white nuchal collar, buffy yellowish forehead and cheeks, tawny flanks and thighs, and bright yellow legs. They look superficially like small falcons (kestrels) and have been so classified, erroneously, by some authors.

In spite of its large range, the species has been little studied. Perhaps this is because the bird is decidedly local and usually uncommon, and builds a small, inconspicuous nest. Apparently the only published breeding record is that of Cherrie (1916), who found a nest (in the Orinoco region of Venezuela) that he collected along with the mother bird, two downy young, and one pipped egg.

It was therefore with considerable surprise and pleasure that I discovered, late in 1969, a breeding pair of Pearl Kites constructing a nest near the top of a casuarina tree (*Casuarina litorea*) less than 100 m (325 ft) from my home at Pointe-a-Pierre on the island of Trinidad. Owing to this fortunate location, and although I had to fit my periods of observation into the schedule of a busy life, I spent well over 100 hours watching and recording the activities of these kites at this and nine subsequent successful nestings between 1970 and 1976.

Because the nests were at the tops of tall flimsy trees, I could not reach them without undue risk both to myself and the birds. I discovered the contents of the nests by using mirrors. With binoculars and a 40-power telescope I studied much of the behavior at the nest while I sat comfortably in a chair in my garage. Although many observations were made randomly,

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Pearl Kite, *Gampsonyx swainsonii*. Painting by Diane Pierce, courtesy of the artist.

I watched for several regular periods (each lasting less than one hour), while on other occasions I watched for long periods of up to 12 hours. I also made many notes on behavior away from the nest, for the kites usually fed and roosted either in my garden or in the vicinity. Although the birds were not marked (banded), I could almost always distinguish between the sexes of the adults by their vocalizations and behavior; the size difference was not generally distinctive in the field.

STATUS OF THE PEARL KITE IN TRINIDAD

Until fairly recently the Pearl Kite was considered a rare visitor to Trinidad, there being only two or three sight records (Herklots 1961). Eight additional records between 1960 and 1964 indicated that the species occurred uncommonly in eastern Trinidad, usually in the vicinity of coconut palms, *Cocos nucifera* (ffrench and ffrench 1966). In all cases single birds were seen.

I first recorded the species near my home at Bonaventure Park, Pointe-a-Pierre, on the western coast of Trinidad, on 4 August 1968, when I heard and saw two birds at the top of a casuarina tree. Intermittent records in the same area in every month until June 1969 led me to believe that the birds had found a profitable feeding area. Although I did not suspect it at the time, I now believe that breeding took place nearby during that period, especially because, on 22 December 1968, three birds were seen calling and chasing each other.

After 6 June 1969 I did not record Pearl Kites at Pointe-a-Pierre until 24 November, and first noted courtship activities in December of that year. During the next six years, ten successful nestings were recorded Table 1), all within an area of 2 hectares (5 acres) and very probably involving the same pair of birds, which remained in residence almost all the time.

Possibly owing to the increasing number of bird observers in Trinidad since the mid-1960's, other regular sightings of the Pearl Kite have been made during the last 15 years, mostly on the eastern side of the island. Additional records of birds seen within a few kilometers of my study area may well have involved the offspring of the Bonaventure pair; also at least two other nests have been recorded in Pointe-a-Pierre within 3 km (2 mi) of Bonaventure Park.

THE STUDY SITE

Pointe-a-Pierre is an extensive suburban housing development adjoining a large oil refinery. Among the houses are well-kept gardens with many ornamental trees, large areas of lawn and open grassland, and an 18-hole golf course. Sizable patches of rough savannah, with isolated bushes and coconut palms, occur on the outskirts. Bonaventure Park lies on the eastern border of Pointe-a-Pierre, and is separated from the large village of Gasparillo by a 4-lane highway that was being constructed during much of the study period. Adjoining the houses with their gardens is an area of open playing fields, comprising some 3.2 hectares (8 acres), bisected and bordered by lines of tall casuarina trees, some of which were used as nest sites by the kites. My house and garden faced a playing field and lay at the end of one line of trees. My garden was dominated by a large hog plum tree (*Spondias monbin*), in which the kites frequently perched for feeding and shelter.

TABLE 1

Pearl Kite Nesting Cycle at Bonaventure Park, Trinidad, 1970–1976

Year	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
1970		[--------3--------]			*******Molt					[--------4--------]		
1971		[--------2--------]				Molt				[--------2--------]		
1972		[----------3----------]			****Molt					[--------1--------]		
1973		[--------3--------]				Molt						
1974			[----------2----------]			Molt						
1975		[--------2--------]				Molt						[---------
1976	---3---]											

[----1–4----] Nesting period from egg-laying to fledging of young; numeral indicates number of young fledged successfully.

********** Unsuccessful nesting attempt.

The human population within Pointe-a-Pierre is fairly thinly spread, and the oil company's ban on wildlife hunting on its property may well have benefited the kites. In a country like Trinidad considerable molestation of birds takes place on a more-or-less casual basis.

Two factors seem to have been particularly conducive to the continued presence of Pearl Kites at Bonaventure Park. First, the casuarina trees were suitable both for nest sites and as lookout stations. The isolation of the trees on the edge of the playing fields also must have reduced the chances of nest predation, particularly by snakes. When, late in 1976, almost all of the trees were truncated drastically in an attempt to eliminate a parasitic vine, the kites were adversely affected and appeared to abandon the area.

Secondly, Pointe-a-Pierre has a considerable population of a lizard, *Anolis aeneus,* which seemed to be the principal food for the Pearl Kites. This Gray Speckled Anole is a fairly recent arrival in Trinidad from the nearby island of Grenada (Boos 1977); it has been found in both suburban and urban districts, especially in gardens, and often displaces less robust competitors. The apparent "explosion" of kites that occurred at Pointe-a-Pierre between 1970 and 1976 may have coincided with a population increase of this lizard.

FOOD

During the entire study period I recorded every food item that I could identify. The most systematic observations were made during the first three nestings, from February 1970 through January 1971; no items were recorded from June through September 1970, when the birds were not nesting (Table 2). The numbers of the two main types of prey recorded are not significant in themselves because the observations were more frequent at some times than at others, but they show the relative importance of lizards and birds in the diet.

It was usually a simple matter to identify lizards as the prey because the tail or legs dangled down in an obvious fashion when a kite flew to a perch carrying a lizard in its talons. I also frequently saw the prey clearly through the telescope from a distance of only 30 m (100 ft) and thus

TABLE 2

Pearl Kite Prey

Item	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*Oct.*	*Nov.*	*Dec.*	*Total*	*% of Total*
Lizards	3	14	22	9	11	6	22	9	96	79.3
Birds	2	0	0	2	0	1	3	2	10	8.3
Unidentified	0	0	4	6	0	1	2	2	15	12.4
Total items	5	14	26	17	11	8	27	13	121	

usually could identify the species as *Anolis aeneus,* the most common lizard in the area. On one occasion I identified a Streak Lizard (*Gonatodes vittatus*). Birds normally could be discerned as such because feathers drifted down from the perch as the prey was dismembered. I identified two food items as Blue-black Grassquits (*Volatinia jacarina*), another as a small brown finch, and a fourth as a young Tropical Mockingbird (*Mimus gilvus*). This last was probably taken from a nest because the kite was pursued by the angry parents as she flew off with the fledgling.

The unidentified items were sometimes small (possibly insects) or shapeless objects with no recognizable feature; at other times the young were already being fed when I began observing, and the prey was no longer identifiable. Occasionally the adult would eat part of its catch elsewhere before carrying the remains to the nest, and I could not identify the prey.

The lizards ranged in length from about 8 to 16 cm (3 to 6 in.), and were usually consumed by the adult birds in 3 minutes. Feeding the young might take up to 10 minutes soon after hatching, but only 2 minutes three weeks later. Birds took longer to be eaten, up to 17 minutes on one occasion. The prey was dismembered by the mother bird, and fed in pieces to the young, each getting some in turn. As the young grew larger, so the morsels increased in size, the last item of a meal frequently being the lizard's hind legs and tail, given all in one piece to one of the young.

On 31 December 1969, before the first nest had been completed, I was watching an adult kite in my garden when it dropped a pellet, the only one I ever found although I regularly searched beneath the nests. Analysis of this pellet showed mostly insect remains, especially from a small terrestrial cockroach, *Pycnoscellus surinamensis,* and also an elaterid ground beetle, *Aeolus* sp. Both insects are common inhabitants of leaf litter in the area. No lizard remains were found in the pellet.

The kites foraged in trees, bushes, and sometimes on the ground. The usual method was for the bird to sit on a high perch and peer down at the surrounding area. Suddenly the kite would dive at a steep angle, to land feet first on a lower branch, occasionally on the ground, and grab its prey. *Anolis* lizards often sit on the outer walls or windows of houses, and a kite would sometimes be seen hunting around the house itself.

VOCALIZATIONS

The typical call of the adult male was a high-pitched musical series of repeated two-syllabled notes, "kitt-y, kitt-y, kitt-y," with the accent clearly on the first syllable. The calls were given as a regular series of from 6 to 15 notes, and were delivered either from a perch or in flight. This call was invariably given when the male brought food for the female. I never heard it given by young birds, but on one or two occasions an adult female called a rather slower version of it.

The most common call given by the female was a plaintive, rather tremulous single note, "whee," fairly long and drawn out. This was often uttered from the nest, but also from a lookout perch when the female was awaiting the male's return with food. The young birds just out of the nest also made this call, but in a slightly higher-pitched and weaker version that was distinguishable only for the first few days. As the young matured, their vocalizations came to resemble the female's more closely.

Another call, given less frequently but by both adults, especially the female, was a shrill whistle, followed quickly by a series of rapid chattering notes falling a little in pitch. This call was given only when one bird seemed particularly excited, as when food was brought after a long interval. The female screamed excitedly when receiving food from the male, and once when she was being mobbed by a group of smaller birds. The young also frequently screamed when receiving food, especially during the fledging stage.

The only other call I heard was once when the female approached the nest to incubate. The male did not move off immediately, and she uttered several soft mewing notes until he did so.

BREEDING

The Nesting Cycle

Ten broods were successfully reared by the pair of kites at Pointe-a-Pierre from December 1969 through February 1976. I can be reasonably sure that the same pair was involved throughout, since I was there almost continuously during the period and never saw behavior indicating the presence of a rival. Also, when the birds were not nesting, they habitually fed and roosted in the area, using favorite perches in certain trees.

Table 1 shows the molting and nesting periods, the former being determined by my direct observation of the birds flying overhead. I recorded only one annual molt, in June, during which the flight feathers were replaced, but I cannot rule out the possibility of another (partial) molt at some other time of year. The number of broods and the actual fledging of 25 young in six years clearly indicates that these kites were outstandingly (and probably unusually) successful during this period.

In their most productive years the kites began to nest in October and completed the nesting process when the young dispersed, about 12 to 14 weeks later. Almost immediately the adults would begin again in February. In two years attempts were made to breed again in May. Both May nests were at new sites and were unsuccessful, although the same sites were used with success in the two subsequent nestings. Apparently the May attempts were terminated by the onset of the molt in June.

In Trinidad the peak breeding months for most land birds are May and June, clearly influenced by the rainy season that begins in May after a dry season of approximately four months (ffrench 1980). A minor peak of breeding also occurs for many passerines in November, often a very wet month, following a lull in the rains that may occur in October.

There seemed, however, to be little correlation between the rains and the kites' breeding cycle. I was also unable to find any weather factor that might explain why the kites bred in October during some years and not others. Indeed, the local climate is comparatively uniform and even when conditions are rainy, dry periods with bright sunshine frequently occur. Temperatures range between 20° and 33°C (68° to 90°F), with little annual variation. The most significant extreme conditions occur in those years when the dry season is prolonged into June or is particularly severe. This did not happen during the period 1970–1976.

Double-broodedness has rarely been recorded in neotropical raptors. Haverschmidt (1968), however, reports one instance in the White-tailed Kite (*Elanus leucurus*) in Surinam, and Brown and Amadon (1968) note that the same species occasionally is double-brooded in California. These second nestings may have occurred in years of abundant food availability, but the correlation is not proved. Similarly, at Pointe-a-Pierre I have no statistics to prove unusual food abundance; but a visiting herpetologist, Robert Holt, noticed that the Gray Speckled Anole, a prinicipal component of the kite diet, was extremely common during my study period.

If one assumes that in double-broodedness the first nest is that following the molt, in two of the kites' three double broods the second clutch was laid in the same nest as the first, but in the third case a different nest was built. Both discontinued nests were reused twice following the next molt.

Courtship

Pair formation evidently had already taken place when I first saw the Pearl Kites near my house. On 4 August 1968 my attention was drawn by the male's call as the two adults were sitting side by side on a high perch. On subsequent occasions a flight display was performed at the beginning of a nesting cycle. The male flew slowly toward the female, calling as he went, and fluttered his wings with a very shallow movement, almost gliding, before landing beside her. Sometimes the female would accompany the male as he fluttered and glided; she would fly above and dive down at him as if in mock aggression. No contact was made. Occasionally copulation would take place soon after this display.

Copulation was observed on 15 occasions. Typically the male would fly directly to the female, who was perched on a casuarina branch, and alight on her back. Sometimes he would first land beside her. On only one occasion did the female initiate copulation, flying down from a higher perch to alight beside the male. She immediately solicited, crouching with tail to one side; the male promptly mounted.

Mating lasted from three to seven seconds. On two occasions, when mating took place twice, the intervals were 20 and 45 minutes. Frequently copulation was associated with courtship feeding, the male having first presented the female with food. Once she was still eating it when he mounted her.

On almost all occasions the copulations occurred at an early stage of the mating cycle. Later on, the female often acted more aggressively toward the male when he approached her.

The Nest

Eight different nests were observed in detail. Six were used only once, and two were used from two to three times in consecutive (successful or unsuccessful) breeding attempts. All nests were in casuarina trees, fitted into the crotches of branches near the top, and often were associated with the tangled growth of a parasitic vine, *Phthirusa* sp., that was growing in many of these trees. The trees ranged in height from about 23 to 30 m (75 to 100 ft), and the nests were situated between 18 and 24 m (60 to 78 ft) from the ground. The trees were too spindly for me to climb to examine the nests from close quarters; therefore, I used mirrors on long poles, and once, by standing in an elevated bucket ("cherry-picker") on the back of an electrical service truck, managed to get to within 5 m of a nest.

All the nests resembled that described by Cherrie (1961), being made of dry twigs, rather loosely put together. The nests were about 20 cm (8 in.) in diameter, with interior cups about 10 cm (4 in.) deep. Most of the twigs were brought from some distance away, so I could not always be sure of their origin, but at least some were from the hog plum or casuarinas because I saw the kites breaking them off in flight. Many twigs brought to the nest measured about 15 cm (6 in.) in length, and several were branched.

Although nest sites varied slightly, the typical nest was wedged between the trunk and the base of a branch, about 5 m (16 ft) down from the top of the tree. Nearby was a tangled clump of the parasitic vine, sometimes in such a position as to provide shelter to the nest, and always assisting in the camouflage of the site.

Both adults cooperated in building the nest, which was constantly being repaired and added to, even when the young were quite large. During incubation, when coming to relieve his mate, the male almost invariably brought a twig unless he brought her food. The female also brought twigs when she returned to the nest. Both sexes broke twigs off branches and seized them with the feet before transferring them to the bill for carrying. In contrast, prey was carried in the feet.

Incubation

The main burden of incubation was borne by the female. She alone incubated at night, and during the day the male covered the eggs only for short periods. When he came to relieve her, either he brought a twig and landed near the nest, waiting until she left before taking her place, or he brought food and called from a distant perch, about 50 m (165 ft) away. She would come for the food and after receiving it, would either fly off to another perch with it or stay at the rendezvous. She never carried it back to the nest. While she ate, the male flew over to incubate.

On 9 February 1970 I watched continuously for 12 hours (from 0630 to 1830) at Nest 1, which contained eggs laid about two weeks earlier. The sun rose at 0622 and set at 1806. During my watch the female sat for a total of 11 hours and 2 minutes (92 percent of the time), in 6 sessions that lasted for 210, 40, 10, 62, 255, and 85 minutes, respectively. The male relieved her five times, his sessions lasting 15, 10, 3, 25, and 5 minutes. On three occasions, at 1000, 1220, and 1700, he brought food for the female. When he brought twigs instead, she left for short periods that hardly gave her time to hunt for herself. She also brought back twigs after each recess.

Throughout the incubation period the female rarely left the nest during the last hour of daylight. Similarly, her first meal of the day often would not be brought until at least two hours after sunrise. Twice I saw the male bring food about one hour after sunrise. The longest recess from incubation I ever recorded for the female was 25 minutes. Much more commonly it was less than 15 minutes. I am fairly certain that during incubation she never hunted for herself.

On only one occasion did the female not incubate the eggs at night. This was when, in an attempt to provide a more permanent method of surveillance, I tied a long pole to the nesting tree. The pole had a small mirror attached at the end, placed so I could observe the contents of the nest from the ground. Although the female sat resolutely while I was putting this arrangement in position, she finally left the nest—about 1745—and did not return that night. Next morning, although she frequently perched nearby, she would not return to incubate. When the mirror was removed later that morning she promptly went back to the nest. The three eggs showed no sign of being adversely affected by this interruption, and eventually three young birds fledged.

Owing to the problems of surveillance, I was unable to determine the exact intervals in which eggs were laid and hatched. I determined the incubation period by observing when the female began constant incubation (apparently always with a full clutch), and when young birds began to be fed. This latter was possible because the adults never fed at the nest during incubation. Thus incubation periods were determined for four broods as 35, 35, 34, and 35 days. I think that some eggs hatched a day or two later than others because I noticed a size difference among members of the larger broods.

Clutches (in 10 nests) ranged from 1 to 4 eggs (mean, 2.5); 8 nests had either 2 or 3 eggs. I found no correlation among the size of the clutch and the time of the year, and whether it was the first, second, or only brood of the year. Eggshells I collected beneath the nests resembled Cherrie's collected specimen; they were dull white, flecked with brown, and measured about 30 × 25 mm.

Of ten other raptor species recorded nesting in Trinidad by Belcher and Smooker (1934), only one, the slightly larger American Kestrel (*Falco sparverius*), produces a clutch exceeding two eggs. The comparatively large clutch size of the Pearl Kites I studied may reflect the local abundance of food. Cherrie's Venezuelan clutch was three, however, so this may in fact be the norm for the species.

The Young

As soon as the eggs hatched, I saw a marked change in the adult kites' behavior. The male brought many more meals for his mate and family, starting early in the morning, and sometimes bringing food three times within an hour. The female spent more time away from the nest than during incubation and occasionally hunted for herself. Sticks for the nest were still brought by the female up to 18 days after hatching, but now the male brought only food.

The usual feeding procedure was for the male to arrive, with the prey in his talons, at a favorite casuarina tree near my house or at the hog plum tree. Soon after the male began calling, the female would fly from the nest to perch beside him. Taking the food with much accompanying squealing, she would return directly to the young at the nest, and the male flew off elsewhere.

On 22 November 1970, when the young in Nest 3 were about 12 days old, I watched continuously for 12 hours, from 0555 to 1755. The sun rose at 0600 and set at 1732. The male brought the first meal at 0639, and the last at 1625. I saw him bring eight meals, and the female two; another three meals were taken to the nest by the female, but it is possible that the male actually provided her with some or all of these, out of my sight. Of the total of 13 meals, 9 were brought between 0639 and 1133, and 4 between 1422 and 1625. A heavy rain shower precluded activity between 1220 and 1300. All the meals were fed to the young by the female, for the male never fed the young at the nest. During the 12-hour watch, the female spent 63.5 percent of the time on or beside the nest: 61 minutes (8.5 percent) she spent actually feeding the young; 4 hours and 48 minutes (40 percent), brooding the young; and 1 hour, 48 minutes (15 percent), standing on a branch beside the nest. She spent the remaining 4 hours, 23 minutes (36.5 percent) away from the nest altogether. Most of the brooding was in the early morning (0555 to 0639), dusk (1630 to 1755), and midday (1220 to 1402), when the weather was heavily overcast or raining.

Although after the young hatched, the male never brought meals directly to the nest, he provided most of the food for the family. Also on occasions, early in the fledging period while the female was away from the nest feeding on her own, he flew to the nest tree and stood on guard. Once, when at least one young bird had hatched, the male brooded for a few minutes while the female was away from the nest.

The Later Stages of Nesting

At hatching, the young Pearl Kites were clad in white down. At the age of 16 days, as the young birds' first contour feathers emerged, dark patches were evident on the upper back and wing coverts; primary wing quills and tail were protruding about 3 cm (1 in.) from their follicles; the head pattern with the black half-collar was already apparent, as were the chestnut-brown upper flank feathers; and the legs were yellow and the gape bright red.

On 20 December 1970 I caught (in a mist net) a young bird that had recently left the nest. It was between five and six weeks old, and seemed fully grown except for the somewhat short tail. It weighed 93 g (3.3 oz). The soft parts were colored as in the adult—chestnut eyes, black bill, and yellow legs. An obvious indication of immaturity was that the edges of the wing coverts and back feathers were tipped with chestnut and white, giving a slightly mottled effect. This bird flew strongly, although its landing on a branch was still decidedly clumsy.

The female parent brooded at night for nearly four weeks after the eggs hatched, but at about 30 days the young started to leave the nest for short periods and moved about in the nesting tree, practicing wingflaps. As long as the young stayed in the nest, the female still tore up prey and distributed it among them. But after they were scattered on different branches, the first bird to get to the food consumed it all.

In most cases the young birds took their first flights at between 33 and 38 days old (mean, 35 days). In two instances I saw birds make short flights of a few meters at 31 days old, but both times this first flight was not repeated that day, and may have been premature. For the first few days after fledging, the young remained in the immediate vicinity, either returning to the nest at night and for food, or being fed at their new locations.

As the young birds began to move around the area, it became impossible for me to keep track of the individuals, except once when I color-banded a fledgling that had left the nest about a week earlier. The adults continued to feed the young for some weeks after fledging was completed, both the male and female bringing food to the nest or nearby. But it was not long before the young started to hunt for themselves, and in most cases the first prey seemed to be insects taken from the ground. I recorded successful hunting of insects by a bird 59 days old, but it also was being fed by the male parent 9 days later.

Some of the young may have dispersed as early as 42 days after hatching. In that instance, I no longer found all the fledged young in the vicinity of Bonaventure Park, and it seemed likely that the more adventurous fledglings had followed a parent to a favorite hunting area about 2 km away. In all cases the young dispersed within ten weeks of hatching, and usually within eight. During the last weeks it was not easy to distinguish the young in the field by plumage, but the plaintive wheezing call note always differentiated them from the adult female.

When two nestings occurred in quick succession, usually about two weeks had elapsed between the last time I saw the fledged young in the area and the first time I noticed the adults showing either interest in a new nest site or courtship behavior. However in one instance a young bird, approximately 61 days old, was seen to be fed on 2 May; two days later it had gone, and I saw the adults performing a series of courtship maneuvers. Nine days after that they began to build a new nest.

The Nonbreeding Season

By early June in each of the years 1970 through 1975, the kites appeared to have begun their molt. During all six "off seasons" they were much less noticeable than when they were nesting. Calling was softer, less insistent, and the female more often used the "kitty" call that I usually associated with the male only.

The pair bond, however, evidently was maintained throughout the nonbreeding period. When they were not nesting, I frequently found the kites roosting side by side on one of the Bonaventure Park casuarinas, and sometimes I saw them flying or perching together during the day. Food-passing was much less common at this time, and once in late August I observed copulation, although nesting did not commence for another six weeks.

Acknowledgments

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Everglade (Snail) Kite, *Rostrhamus sociabilis*. Painting by George E. Gilbert, courtesy of Arlene E. Saunders.

Burrowing Owl (*Athene cunicularia*). Pen and ink with ink wash drawing by David Maehr.

THE BALD EAGLE CONCENTRATION IN GLACIER NATIONAL PARK, MONTANA: ORIGIN, GROWTH, AND VARIATION IN NUMBERS

B. Riley McClelland, Leonard S. Young, David S. Shea,
Patricia T. McClelland, Harriet L. Allen, and Elizabeth B. Spettigue

Spawning runs of Pacific salmon (*Oncorhynchus* spp.) attract migrating or wintering Bald Eagles (*Haliaeetus leucocephalus*) along a number of rivers and lakes in northwestern North America. The eagles gather to feed where spawned-out salmon are accessible and human disturbance does not exceed the eagles' tolerance level. In Glacier National Park, Montana, an autumn concentration of Bald Eagles developed after the mid-1930's, when spawning of introduced Kokanee Salmon (*O. nerka*) was first reported from lower McDonald Creek. The number of Bald Eagles there has since increased dramatically. During the autumns of 1978–1980, the mean maximum count was 503, primarily along a 4-km (2.5-mi) stretch of lower McDonald Creek in the southwest corner of the park.

In this paper we discuss the origin and growth of the concentration and present hypotheses concerning changes in the number of eagles present in autumn. We also offer speculations on how eagles discover and capitalize on new food sources. Our data and interpretations are based on 16 years (1965–1980) of research on the Glacier concentration. Brief summaries of the concentration were reported for 1965–1970 by McClelland (1973) and for 1971–1977 by Shea (1978).

BACKGROUND OF THE STUDY

The fall migration of Bald Eagles through Montana generally occurs from September through late December. Within their migratory and winter ranges, eagles tend to congregate in large numbers at sites where food is abundant, and to occur singly or in small groups where it is more limited. During January 1981, 13,709 Bald Eagles were counted in the conterminous 48 states (Anon. 1981a). Approximately 25 percent of these wintered in the Northwest (Washington, Oregon, Idaho, and Montana), with a total of 421 in Montana. The number that migrates through the state is undoubtedly much higher.

Salmon spawning runs have attracted Bald Eagles for centuries. All Pacific salmon (five species native to North America) die after spawning, providing a food source to which eagles and other wildlife are drawn. Dawson and Bowles (1909: 520) wrote: "Fifty years ago they [Bald Eagles] existed on Puget Sound and along the banks of the Columbia in almost incredible numbers... they could obtain all the fish they wanted...." Signif-

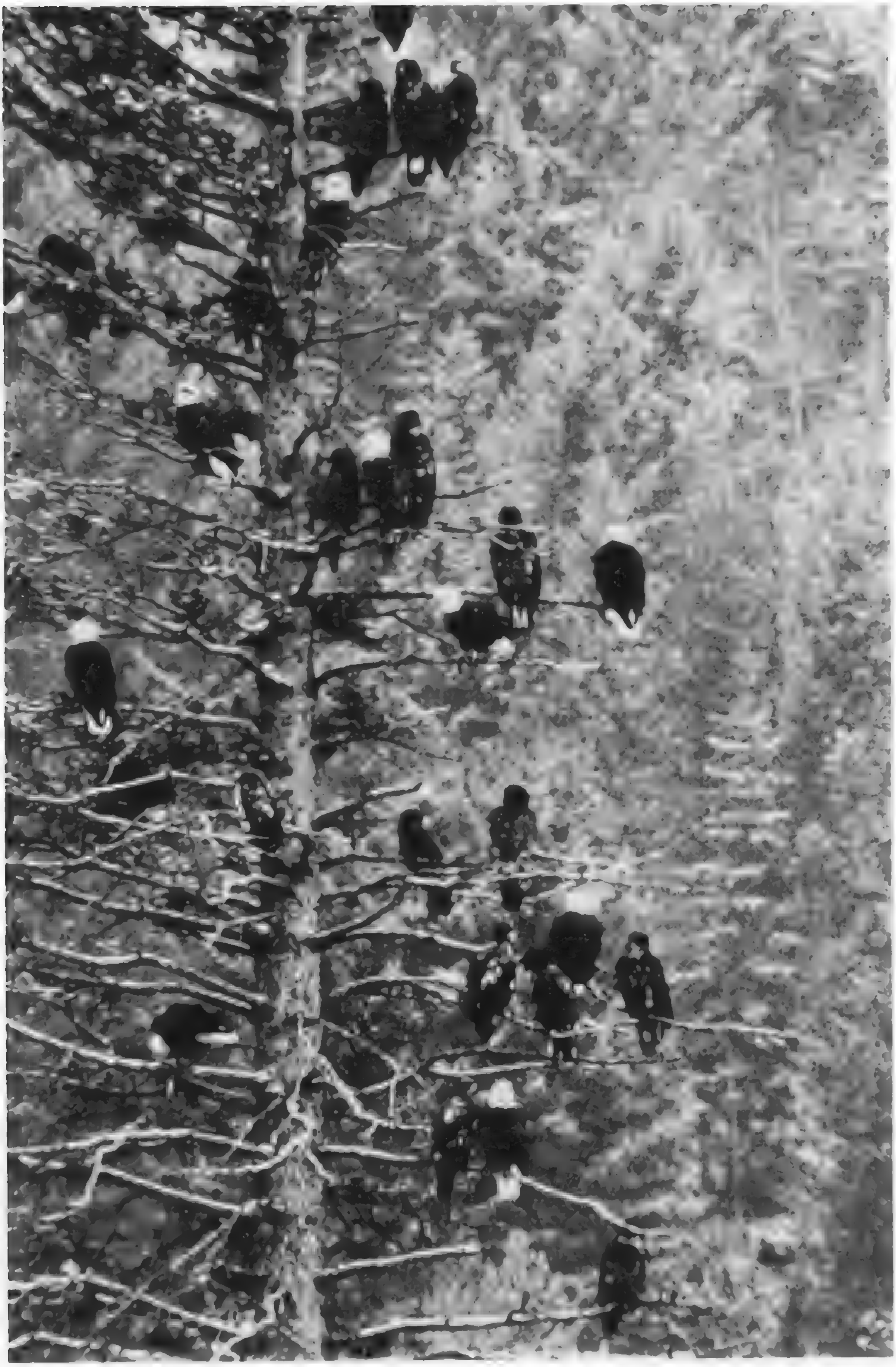

Figure 1. Bald Eagles congregate along lower McDonald Creek to feed on Kokanee Salmon. Photo by B. R. McClelland.

icant concentrations of Bald Eagles still occur at natural salmon runs along several western rivers, including the Skagit and Nooksack (Washington), the Fraser (British Columbia), and most notably the Chilkat in Alaska, where more than 2,800 eagles have been counted at the autumn concentration (Boeker et al. 1980). However, more than half of the habitat in the Columbia River watershed (seven states and British Columbia) originally accessible to salmon is no longer available or suitable. This loss is the result of dam construction, water quality changes, and human disturbance (Stalmaster and Newman 1978, Netboy 1980, Skagen 1980, Knight 1981).

The substantial decline in original salmon habitat and eagle feeding opportunities has been offset to some degree by other human activities. Several Columbia River tributary systems, originally inaccessible to salmon from the ocean because of natural barriers, now support populations of landlocked Kokanee Salmon introduced by man. Spawning runs in two north Idaho lakes, Coeur d'Alene and Pend Oreille, attract Bald Eagles in the late autumn or early winter (Lint 1975). Between 40 and 70 eagles have been counted at Lake Coeur d'Alene in November and December of recent years. In late December 1980, 123 eagles (feeding on waterfowl as well as salmon) were counted at Lake Pend Oreille (Louis Brown pers. comm.).

In lower McDonald Creek, Glacier National Park, Kokanee established annual spawning runs by at least 1935, as a result of introductions in Flathead Lake, 96 km (60 mi) downstream, in 1916, and in Lake McDonald, immediately upstream, in 1922 and 1923. Park rangers who routinely patrolled the McDonald Creek Valley from 1910 on, did not record more than an occasional Bald Eagle until 1939, when they counted 37. Nearly four decades later, on 29 November 1978, we counted 618 eagles, most of them along lower McDonald Creek. From the arrival and departure patterns of the birds, we believe that during the fall of 1978, more than 1,000 Bald Eagles stopped at this site before continuing on to more southerly wintering areas. Thus, within this short span of time, the lower McDonald Creek Valley has changed from an area through which only a few eagles presumably passed each year, to its current status as a major feeding stop for migrants (Figure 1). The concentration, which peaks in November, probably represents the highest density of the species at any site in the conterminous United States.

STUDY AREA AND METHODS

Study Area

Glacier National Park (48° 30′ N, 114° 00′ W) is bisected by the Continental Divide (the Rocky Mountains) and bounded on the north by the border between Canada and the United States (Figure 2). McDonald Creek, in the park's southwest corner, is the central feature of the study area (Figure 3). Upper McDonald Creek originates on the west slope of the Continental Divide and flows into Lake McDonald (16 km long, 1.2 km wide; 10 × 0.7 mi). Lower McDonald Creek flows from the lake for 4 km (2.5 mi) before joining the Middle Fork of the Flathead River at the park boundary. It eventually becomes part of the Columbia River and ultimately the Pacific Ocean.

Vegetation within the eagle concentration area has been briefly described by McClelland (1973) and Shea (1978), and in detail by Habeck (1970). The eagles use several tree species for perches along the creek, especially Western Larch (*Larix occidentalis*), Western Redcedar (*Thuja plicata*), and Black Cottonwood (*Populus trichocarpa*).

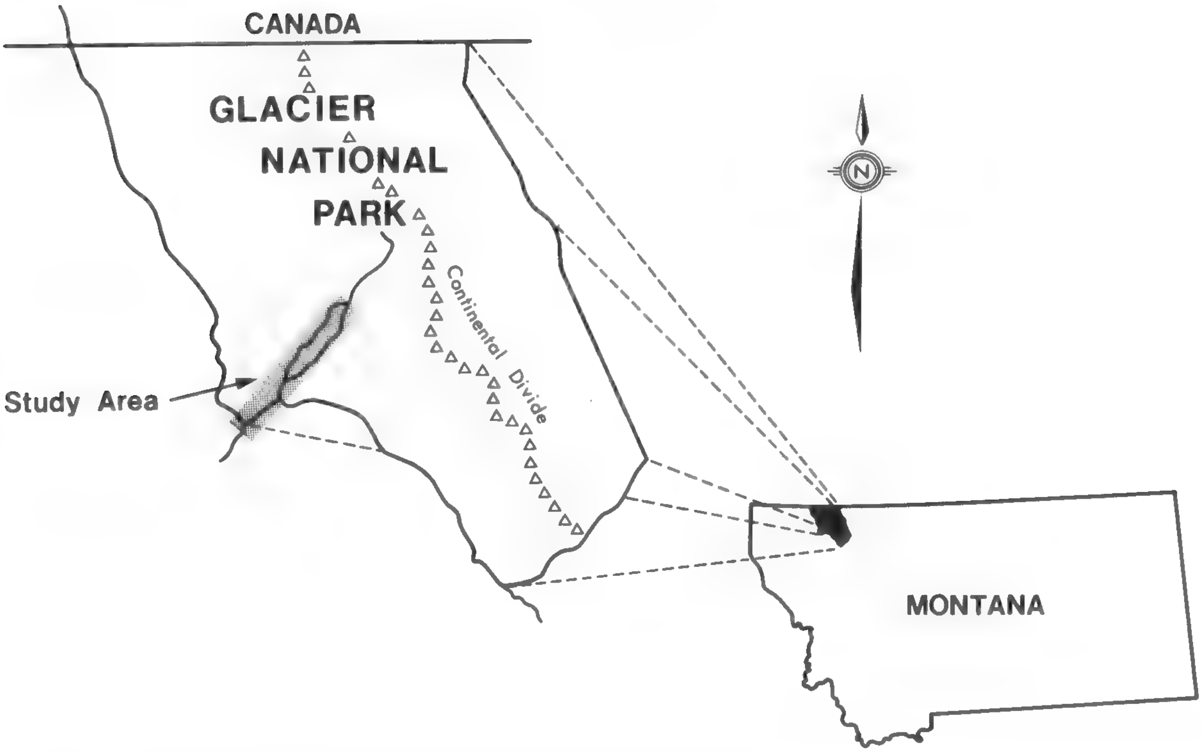

Figure 2. Glacier National Park and location of study area.

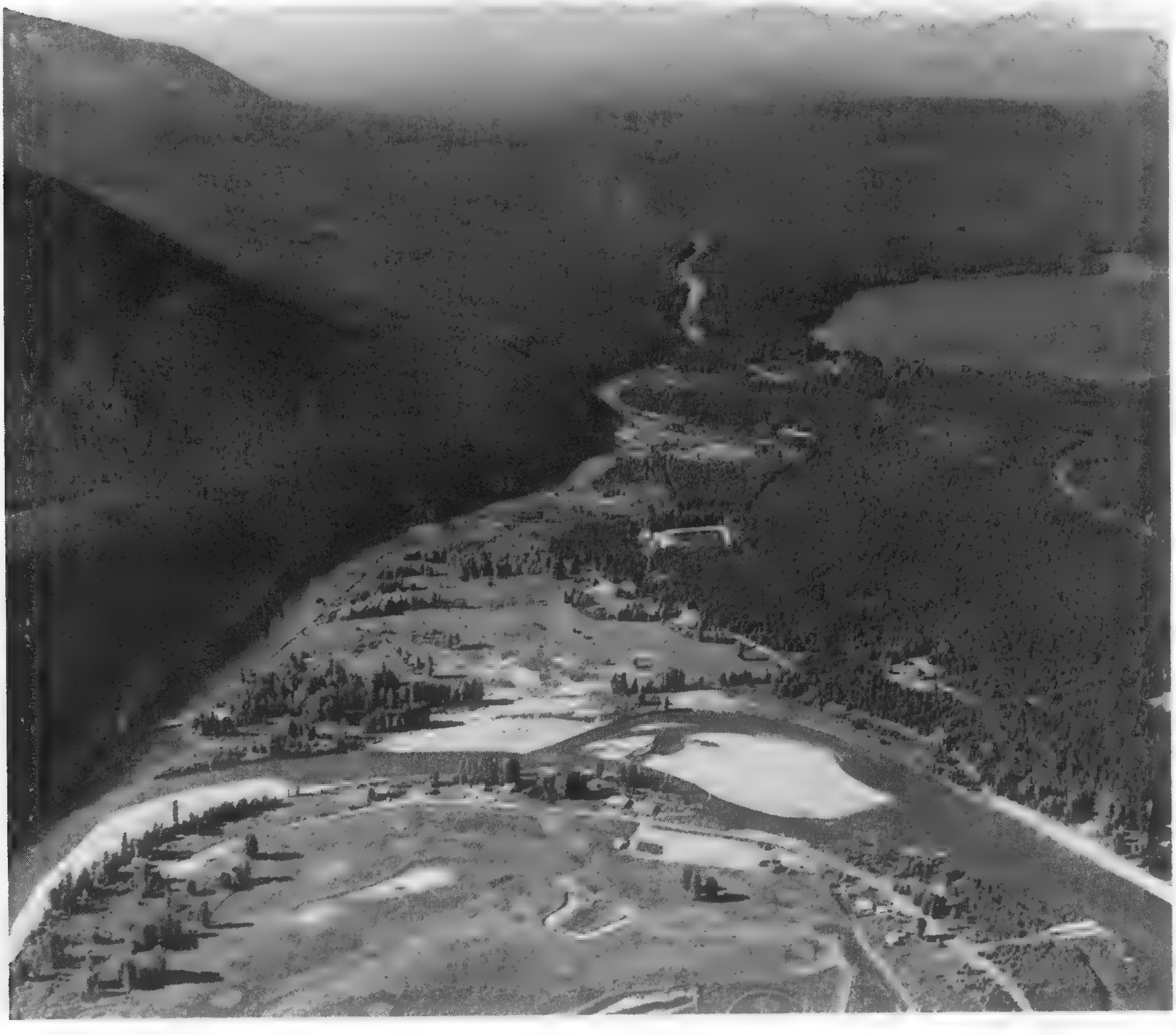

Figure 3. Lower McDonald Creek flows from Lake McDonald (upper right) to join the Middle Fork of the Flathead River (at lower left). Photo by B. R. McClelland.

Counting Procedures

Since 1965 we or National Park Service (NPS) personnel have conducted weekly counts of Bald Eagles in the study area during autumn. Our counts usually extended from September through December. During 1967 and 1973–1976 NPS personnel counted but did not include all early or late autumn periods. The purpose of the counts was to provide information on long-term trends in numbers, changes in age-group ratios, changes in spatial and temporal patterns of the eagles, and locations in need of special management measures. Each year we covered the 4-km stretch of lower McDonald Creek (Figure 4, Section 2), along which about 90 percent of the eagles have consistently been found. Unless fog delayed departure time, counts began in the morning as soon as there was adequate light. Calm mornings were selected whenever possible because of the tendency of eagles to soar during wind.

Some modifications have been made in the counting method since it was first described (McClelland 1973). Beginning in 1977 we consistently also surveyed Lake McDonald (Figure 4, Section 1) and counted eagles from a point overlooking a major perching area along the Middle Fork of the Flathead River (Figure 4, Point E). However, tallies throughout 1965–1980 remained comparable; the additional count areas may have increased totals by roughly 10 percent.

Our procedure was as follows (refer to Figure 4): One day a week the count began from a canoe at the outlet of Lake McDonald (Point A). At the same time, another observer started the Lake McDonald count, coordinating with the canoe counter to avoid duplication at the outlet. The lake counter proceeded northeast along the lake as the canoe floated southwest down the creek. Only those eagles that were passed by the canoe were counted. An observer at Point E counted all eagles in view along the Middle Fork of the Flathead, completing the count before eagles flushed by the canoe flew downstream. A counter at Point D (bridge over lower McDonald Creek) tallied eagles flushed downstream ahead of the canoe. The canoe continued through Section 3, but the count from this section was used in the total only if it exceeded the counts from Points D plus E, in which case it was used in lieu of those figures.

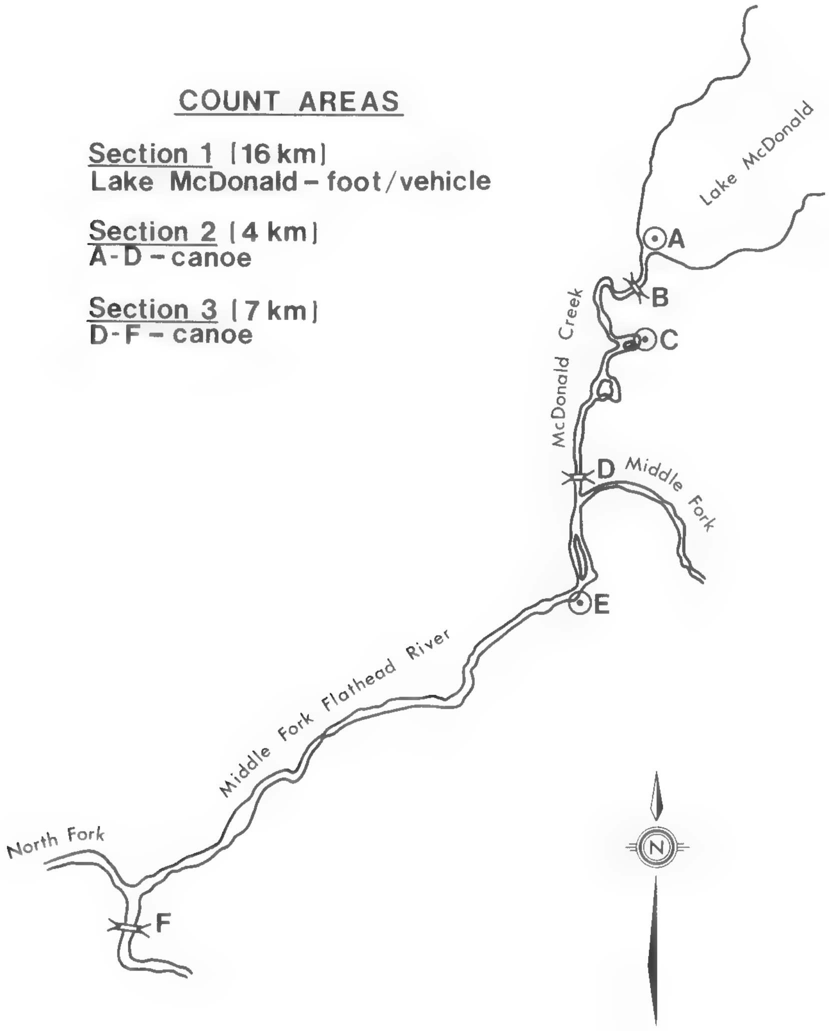

Figure 4. Count area, sections, and points used in Glacier Park eagle census.

Counts were conservative and there was little chance of duplication. Although most eagles perched near the water, some were out of view and undoubtedly were missed. The method of counting did not produce precise numbers, but it was conducted in a consistent manner so that weekly and annual comparisons would be meaningful.

Before 1965, counts were made on foot and no standardized routes were used. Some eagles probably were counted more than once during a given day because of the difficulty of keeping track of their movements while the observer was traveling from one counting point to the next. Therefore, pre-1965 data may contain some overestimates.

We conducted most of our field observations (as opposed to counts) from a blind at the "oxbow" (Figure 4, Point C) or from the bridges at either end of lower McDonald Creek (Figure 4, Points B and D).

Age-Class Criteria

"Adults" and "subadults" were the only age classes used during counts. Eagles with a dark body and an all-white head and tail were recorded as adults. All others were considered subadults. The distance at which some of the birds were seen, and the necessity for counting rapidly as the canoe proceeded downstream, made impractical any further subdivision of subadults into plumage or age classes. Additionally, many inconsistencies arise when one tries to correlate plumage characteristics, age class, and breeding capability (Sherrod et al. 1976). There may be no consistent relationship among the three because the physiological condition of individual eagles, environmental factors, and opportunities for entering the breeding pool vary (Newton 1979). Most Bald Eagles, however, are at least five years old before they attain a fully white head and tail.

Data Calculations

Calculation of the percentage of subadults in a single count was straightforward. However, the percentage for a series of counts during a season could be calculated in three different ways: based on the day on which the largest total number of eagles was counted; based on the maximum number of subadults and maximum number of adults, though they occurred on different count days; and based on the total number of adults and of subadults from all counts during the year. We report the results from each method, as well as an approximation of total eagle use days (EUD)[1] for each season. Although the EUD values derived were not precise, they provided a consistent way of quantitatively comparing eagle use (incorporating both numbers of eagles and duration of eagle presence) among years. Use days did not give any indication of the total number of different eagles involved; turnover time for individual eagles may have been short.

FOOD: THE FOUNDATION OF THE CONCENTRATION

The food base that attracts the eagles, Kokanee Salmon, is available for two or three months each year. The first Kokanee usually appear at the mouth of lower McDonald Creek in September. Full scale spawning begins in gravel under running water in October and continues well into November. Rarely, some spawning occurs as late as January.

Estimates of the number of salmon spawning in McDonald Creek range from 75,000 to 125,000 in the late 1960's, to 45,400 in 1980 (data from the Montana Dept. of Fish, Wildlife and Parks). This magnitude of variation in the estimates may, at least in part, be a result of inconsistent data-gathering. Estimates made in the 1960's were based on observations made while walking along the creek; estimates in 1980 were

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[1] Eagle use days were calculated as follows:

$$\mathrm{EUD} = \sum_{i=1}^{n-1} d_i \left(\frac{c_i + c_{i+1}}{2}\right)$$

where d = number of days betwen count i and i + 1; i = count number; n = number of counts; and c = number of eagles seen on a given count.

based on a snorkeling census. Although the precise number of salmon that spawn in McDonald Creek is unknown, it varies widely from year to year, probably by 100 percent or more. In years when Kokanee are larger than average, there tend to be fewer fish.

All of the salmon die within two or three weeks after spawning. After death, they tend to float downstream before lodging on a shallow area or sinking to the bottom of a deep pool. By mid-November salmon carcasses nearly cover the stream bottom in deep pools and quiet water. Eagles either wade into shallow water or stoop for dead or dying fish that are floating.

Decomposition of salmon caracasses is rapid. By early January few can be seen and the eagles have moved on toward their ultimate wintering sites.

EAGLE DISCOVERY OF THE SALMON RUN

During the early years (the late 1930's) of the autumn salmon spawning run in Lower McDonald Creek, discovery by eagles apparently resulted from chance or by searching of migrants or the few resident eagles. If McDonald Creek had been on a consistently used migration corridor, rapidly increasing numbers of eagles should have been detected within the first few years. This did not occur (Table 1). Instead, there were low numbers of eagles through the 1940's and 1950's, followed by steadily increasing numbers in the 1960's and 1970's.

The presence of other, more numerous, local scavengers—Common Crows (*Corvus brachyrhynchos*), Common Ravens (*C. corax*), Black-billed Magpies (*Pica pica*), and Coyotes (*Canis latrans*)—that would

TABLE 1

Maximum Number of Bald Eagles in a Single Count in the McDonald Creek Area, Glacier National Park, 1965–1980

Year	*Number of eagles*	*Year*	*Number of eagles*
1939	37	1960	no report
1940	24	1961	no report
1941	20	1962	178
1942	30	1963	352
1943	30	1964	134
1944	14	1965	189
1945	10	1966	179
1946	17	1967	211
1947	20	1968	234
1948	14	1969	373
1949	25	1970	268
1950	20	1971	267
1951	59	1972	261
1952	no report	1973	357
1953	53	1974	359
1954	86	1975	377
1955	82	1976	361
1956	47	1977	444
1957	no report	1978	618
1958	no report	1979	516
1959	16	1980	377

have discovered the salmon quickly, should have served as a signal to any eagle searching off of a primary corridor. Such corridors are along the Flathead River to the west and along the front range of the Rocky Mountains to the east. Any eagle discovering the salmon would probably have returned to the spawning run during subsequent fall migrations.

It was not until the early 1960's, nearly 30 years after the first salmon run, that the number of eagles began to increase at the site (Table 1). As the number of eagles soaring over McDonald Creek grew, the likelihood of their being seen by distant migrating eagles increased. The group soaring phenomenon may have been the key to attracting many "new" eagles to the concentration.

Discovery by Sight Detection

Craighead (1980) and others have speculated about eagles keying into concentrations by using visual cues. Eagles have excellent visual acuity (Sillman 1973, Brown 1977); evidence includes Shlaer's (1972) measurements of retinal image quality in the Congo Serpent Eagle (*Dryotriorchis spectabilis*) and behavioral testing of visual acuity in the American Kestrel (*Falco sparverius*) by Fox et al. (1976). Shlaer concluded, on the basis of eye size, that the eye of a Golden Eagle (*Aquila chrysaetos*) might surpass human resolution by a factor of 2.9. Fox et al. concluded that the kestrel's acuity was about 2.6 times that of a human. Both Shlaer and Fox et al. pointed out the difficulty in specifying all of the optical and neural factors that contribute to hyperacuity. Neither of their investigations supported the contention of Walls (1942) and Brown (1977) that eagles may see detail up to 8 times as fine as humans can; but one might infer from the example given by Fox et al., in which "larger Falconiformes" can detect prey 16 cm (6.3 in.) long at an altitude of 1,500 m (4,900 ft), that one Bald Eagle could detect another at a distance of at least 19 km (11.8 mi).

Soaring

Soaring appears to have several functions: it enhances visibility for prey searching (Pennycuick 1973) and provides a "stage" for courtship and communication (Brown 1977, Newton 1979); it may also serve to advertise a discovered food source to other, distant eagles (Servheen and English 1979 and citations therein).

Group soaring against an open sky also makes eagles conspicuous and visible at much greater distances than when the background is dark—as with vegetation or the ground—and enhances the possibility of long distance detection of one flying eagle by another.

Hailman (1977) suggested that animals habitually signalling against homogeneously light backgrounds are usually totally dark or dark with white signal patches. He further stated (p. 222): "Animals signaling with a background such as sky ... tend to have achromatic signal coloration. Theirs is largely a world of black and white." The adult Bald Eagle plumage patterns—white head and tail and otherwise dark brown—is advantageous for such signaling.

Armstrong (1971: 534) wrote concerning social food signaling: "... white coloration of some ... species serves as an automatic signaling device indicating to other individuals areas in which a comparatively abundant food supply is temporarily available." Group soaring may thus effectively signal sites of abundant food to other eagles some distance away.

Distance vision experiment.—We hypothesized that Bald Eagles migrating south from Canada along favorable wind corridors many kilometers west or east of McDonald Creek, might be attracted to the salmon run by eagles soaring over the creek. But at how great a distance might one eagle detect another—alone or in a group? Although we do not have sufficient evidence to provide a definitive answer, we offer a rough estimate of the range of distances at which one Bald Eagle might see another. We used a crude method similar to that described by Brown (1977: 54) to derive the estimate:

A small two-dimensional outline of a Bald Eagle was cut to scale and the appropriate portions (wings and body) were darkened, leaving the head and tail white. The wingspread was 42.6 mm (1.7 in.), a ratio of 1/50 in relation to actual wingspread of the largest adult Bald Eagle we have captured and measured (N=10) for a different study at McDonald Creek. We then determined the mean maximum distance at which observers (three) could see the cutout against a blue background (simulating clear sky) and against a white background (simulating cloudy sky) (Table 2, Line A). In both tests the cutout was projected out on a small diameter wire, so that it appeared isolated in the sky. The wingspread of the "eagle" was positioned with its plane perpendicular to the observer's line of sight. This is the attitude in which the eagle would be most easily seen by another bird and through which a soaring eagle commonly passes.

We then determined the distance at which a real eagle (50 times larger than the cutout) might have been seen by the observers under the same circumstances (Table 2, Line B). Finally, multiplying the distance at which human observers could see a real eagle by the superiority factors of eagle visual acuity, the 2.9× suggested by Shlaer (1972) and the 8× claimed by Walls (1942), we arrived at a range of the estimated distances at which one Bald Eagle might see another. Although this is an admittedly crude attempt to quantify visual detection distances for Bald Eagles, the results suggest that the possibility of long range detection is real. Our calculations indicate that against a bright cloudy sky, visual detection may range from 23 to 65 km (14 to 40 mi). The actual distance may not often approach the higher figure, but probably easily exceeds the lower. These distances are

TABLE 2

Determination of Hypothetical Distance at which One Eagle may see Another Eagle Soaring

Measurement	*Against white (cloud) background*	*Against blue (sky) background*
A) mean maximum distance seen by (3) human observers	163 m	115 m
B) distance at which an adult Bald Eagle would be visible to human observers (A × 50)	8150 m	5740 m
C) distance at which one eagle may see an adult eagle soaring		
B × 2.9 (Shlaer 1972)	23.6 km	16.6 km
B × 8 (Walls 1942, Brown 1977)	65.2 km	45.9 km

based on viewing a single eagle. When many eagles soar together, detection distance would be increased because several adjacent eagles in the soaring group would blend visually (at a distance) to make a larger "spot" in the sky.

We know that many southward migrating eagles move down the North Fork of the Flathead River, which would bring them within 9 km (5.6 mi) of McDonald Creek. If they did not already know about the concentration (from their visits to the salmon run in previous years), they almost certainly could see soaring eagles from that distance. Eagles migrating along the Continental Divide, 22 km (13.7 mi) from lower McDonald Creek, or even along the east slope of the Rocky Mountains, a raptor flyway 45 km (27.9 mi) from the creek, conceivably also could see eagles soaring above the concentration area.

The distance at which soaring eagles can be seen by other eagles undoubtedly varies widely, depending on such factors as atmospheric conditions and light. We have noted several factors that would increase the possibility of long-distance sighting during the Glacier concentration. Eagles along McDonald Creek tend to soar on windy days, particularly in the afternoons; migrating eagles are most likely to be moving at these times. Soaring at McDonald Creek usually is a group activity, with as many as 100 eagles flying together in an area sufficiently small that their massed bulk would enhance detection from a distance. Both soaring and migrating eagles often attain an altitude of 2,000 m (6,560 ft) or more above the terrain in the vicinity of Glacier Park; this also should enhance visibility. We conclude that sight, in itself, may be sufficient to lead migrating Bald Eagles to the concentration.

Discovery by Following Other Eagles

Some subadult birds, particularly eagles less than a year old that have not previously visited wintering sites, may follow adults or other subadults during the autumn movement south. After eagles have found favorable wintering areas (with a suitable food supply), most individuals probably return there for at least part of the winter in subsequent years (Gerrard et al. 1978). An eagle on which we placed patagial wing-markers in 1977 in Glacier has been seen during three consecutive winters at Malheur National Wildlife Refuge in eastern Oregon, as well as each autumn at Glacier, while en route to Malheur.

Eagles on their way to a predetermined destination may exhibit a "purposeful flight," detectable to other eagles; subadults and others without a specific destination may respond by following (Servheen and English 1979, Craighead 1980). Houston (1974:68) described the way in which griffon vultures (*Gyps* spp.) in the Serengeti National Park, Tanzania, may be drawn from at least 35 km (22 mi) to a food source: "Once a bird sees a source of food its flight path changes from a slow, wandering flight into a direct dive toward the food. This rapid, direct flight path is very conspicuous and neighboring birds within sight also start to descend in the direction the first bird is heading, although they themselves may not be able to see the food. Vultures out of sight of the first bird, but within sight of the followers, also notice the change in flight behaviour and start to follow, and so a chain reaction radiates out from the food site."

Following could also occur from chance encounters along a migration corridor. During long-distance movements, what appears to be a solitary flight by an eagle, may not be that at all. With the ability of eagles to see great distances, subadults that seem to be migrating alone may, in fact, be following another eagle or eagles at a distance too great for human perception.

Discovery Through Information Transfer at Communal Roosts

Information on food availability and location may be transmitted among birds at communal roosts or at other areas of aggregation (Ward and Zahavi 1973). The suggested information-transfer mechanism is that in departing from a roost, individuals with low previous success in feeding may join individuals or groups whose behavior and (or) appearance indicates (or has indicated) prior feeding success and impending return to an area where food is available. Several authors have suggested that information transfer may apply at communal roosts of Bald Eagles (Hansen 1977, Hansen et al. 1980, Knight 1981) and other raptors (Gurr 1968).

Information fundamental to migration may also be transmitted at communal roosts. Several workers have postulated or demonstrated that roost behavior may coordinate or stimulate migration in non-raptors (Swinebroad 1964, Richardson and Haight 1970, McIntyre 1978), and Meinertzhagen (1956) suggested that communal roosts of Montagu's and Marsh harriers (*Circus pygargus, C. aeruginosus*) may facilitate communal migration by providing the means of congregation for these usually solitary raptors.

Although no-one has demonstrated that food information gained much earlier may be transferred, perhaps months later, to roost associates, we believe that integration of the two hypotheses is reasonable. This synthesis suggests that information regarding the location of geographically remote temporary food sources (such as Glacier's salmon) may be transmitted at communal roosts used before and during migrations. Thus naive eagles may follow those with previous experience at the salmon run to lower McDonald Creek, by keying in on behavioral cues transmitted at, or in the immediate vicinity of, communal roosts used before arrival at Glacier. Some of the eagles that visit the Glacier concentration are known to roost communally during migrations (Young pers. obs.).

EAGLE NUMBERS AT THE CONCENTRATION

Although the long-term increase in the number of eagles attending the McDonald Creek spawning run (Table 1) probably has resulted from some form of communication among eagles, year-to-year changes in their numbers also are affected by changes in the level of human disturbance in the feeding area or by variation in available food (the number of accessible salmon).

Human Disturbance

That human disturbance can displace Bald Eagles from feeding sites is well documented (e.g. Stalmaster and Newman 1978, Skagen 1980). The reverse may also be true: when a section of the Columbia River in Washington was closed, the resulting reduction in disturbance may have accounted for the increase in eagles there in the 1960's and 1970's (Fitzner and Hanson 1979). Human disturbance along lower McDonald Creek was markedly reduced beginning in 1970, when the area was closed to the public each year during the eagle concentration. During the 1970's, when McDonald Creek was a more protected feeding site for eagles, the Middle Fork of the Flathead River (Figure 4) was heavily used by "salmon snaggers" and hunters. Eagles now have little opportunity to avoid humans along most of the Middle Fork immediately downstream from McDonald Creek. The protection from disturbance at one site and the increased disturbance at the adjacent river probably have both been factors in the increased number of eagles along McDonald Creek.

Relationship with Salmon Abundance

The relationship between numbers of eagles and availability of fish has been noted by many authors (e.g. Southern 1963, Hunt et al. 1980). Between 1978 and 1980 the maximum count of eagles in Glacier decreased 39 percent (618 to 377). This decrease probably was largely influenced by a strong decline in the salmon run in 1980. Fewer fish were in the run, and the period of time during which salmon carcasses were available was much shorter than in 1978. Census results from 1978 (salmon abundance) and 1980 (salmon paucity) illustrate the contrasting patterns in duration of eagle presence and number at the peak count (Figure 5). Both years show the rapid decline in eagles as salmon carcasses become less numerous late in the season.

Quantitative data are not available on the size of salmon runs in McDonald Creek for most years, but qualitative estimates during our 16 years of study indicate a direct relationship between the abundance and duration of availability of salmon, and the number of eagles at peak counts.

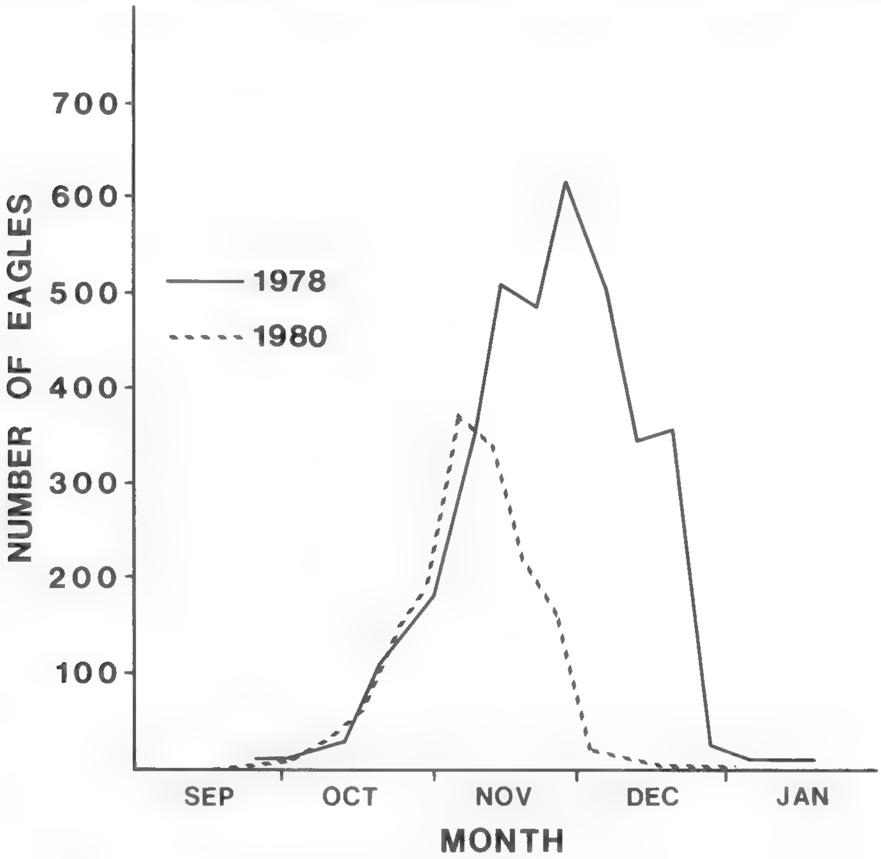

Figure 5. Bald Eagle census results, 1978 and 1980.

Lower peak counts in recent years may not be related to fewer eagles visiting the concentration, but rather to their not lingering at the creek when salmon were not abundant.

Eagle Use Days and Salmon Consumption

Eagle use days (EUD) generally have increased since 1965, as one would expect from the trend of higher peak counts. However, the duration of the concentration also has increased (although it dramatically shortened in 1980), bringing about a relatively greater change in EUD than in peak counts (Figure 6).

Mean EUD for the 11 years shown in Figure 6 is 11,015 (only data from those years in which counts began early and ended late in the season were calculated: 1965–1966, 1968–1972, 1977–1980). During the first three of those years the mean was 4,410 EUD; during the last three years it was 19,431 (more than four times greater).

Based on energetics information and our approximation of EUD, we estimated the number of salmon necessary to provide a maintenance level of energy for eagles:

The mean weight of a single Kokanee Salmon from lower McDonald Creek is approximately 254 g (8.9 oz) after spawning (estimate from Montana Dept. of Fish, Wildlife and Parks, based on 17 years' data). In some years the salmon are considerably larger (Table 3). Captive Bald Eagles studied by Chura and Stewart (1967) consumed a (primarily salmon) diet that averaged 264 g daily. From laboratory and field data, Stalmaster (1981) calculated that a wild eagle (4.5 kg, 9.9 lb) needs 500 g (17.5 oz) of salmon daily to meet its energy requirements. Based on this figure, we

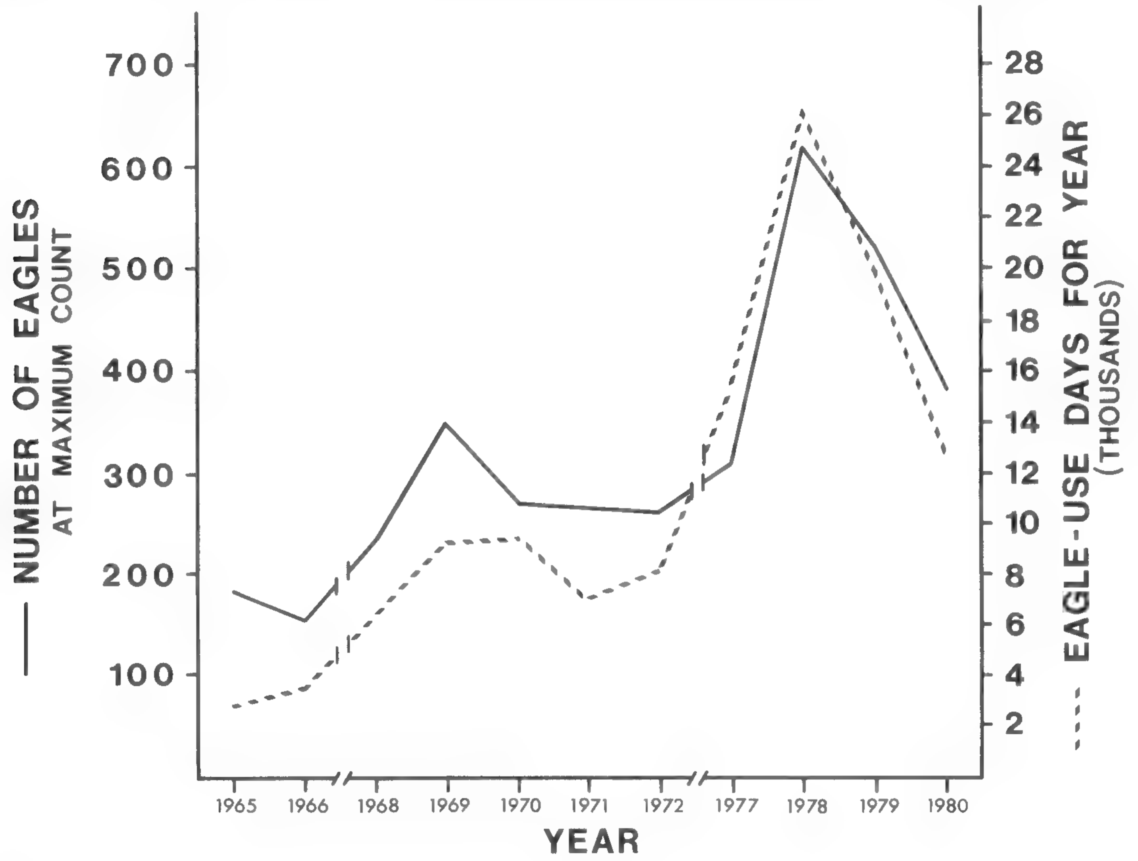

Figure 6. Peak counts and eagle use days (EUD) at the Glacier concentration. Only data from those years in which counts began early and ended late in the autumn are shown.

TABLE 3

Eagle Use Days and Energy Requirements in the McDonald Creek Area

			Number of salmon[2] *required to meet daily energy requirements*	
Year[1]	*Eagle use days*	*Mean wt. of salmon (g)*	*Daily per eagle*	*Season (all eagles)*
1965	2,900	269	1.86	5,394
1966	3,774	199	2.5	9,473
1968	6,556	141	3.55	23,274
1969	9,397	226	2.21	20,767
1970	9,432	269	1.86	17,544
1971	7,142	287	1.74	12,427
1972	8,321	287	1.74	14,479
1977	15,349	292	1.71	26,246
1978	26,035	284	1.76	45,822
1979	19,797	323	1.55	30,685
1980	12,460	380	1.32	16,447

[1] Only years in which counts extended from early to late in the season are included.

[2] Based on mean salmon weight for the season.

estimate that a Bald Eagle at McDonald Creek would need to consume about two salmon each day to maintain its weight. This assumes that the energy value of Kokanee Salmon is similar to that of the Chum Salmon (*O. keta*) used by Stalmaster. At the peak count of 618 eagles (in 1978), 1,236 salmon would have to have been consumed in a day if minimum energy requirements were being met and salmon were of average weight.

From field observations, Shea (1973) estimated that eagles at McDonald Creek consume five or six salmon each day. That eagles are capable of eating that many large fish is suggested by Shea's watching one individual consume three salmon within 45 minutes. Based on Shea's data, between 3,090 and 3,708 salmon would have been consumed on the day of the peak count in 1978, when 618 eagles (441 adults) were present. Subadults, however, often consume less than adults do (Stalmaster 1981), so the total number of fish taken may have been considerably lower.

The consumption rate for adult eagles at McDonald Creek appears to exceed the minimum needed by 100 percent or more during the period of maximum salmon abundance. Thus, many eagles seem to be building energy reserves rather than simply meeting their daily maintenance requirements. The Glacier spawning runs provide an opportunity for eagles to build reserves that may sustain them through the remainder of migration to their winter destinations.

The number of salmon necessary to support the large number of eagles of recent years is impressively high (Table 3). We calculate that the number of salmon needed by eagles for maintenance energy alone appears to be approaching a high proportion of the total number of salmon spawning in the creek. The eagle concentration may now have reached a food-limited state.

TABLE 4

Dates of High Counts (bold face) for Adults and Subadults

Year	*Date*[1] *(November)*	*Adults*	*Subadults*	*Unknown age class*	*Total eagles for date*	*Total eagles based on maximum number adults & subadults*
1965	19	**98**	**58**	33	189	189
1966	3	82	**69**		151	185
	10.	**116**	58	5	179	
1967	17	76	**74**		150	225
	28	**151**	60		211	
1968	21	**150**	**84**		234	234
1969	20	**253**	**117**	3	373	373
1970	22	129	**97**		226	280
	25	**183**	85		268	
1971	10	112	**133**	22	267	257
	17	**124**	106	2	232	
1972	9	**174**	**87**		261	261
1973	7	151	**177**		328	407
	20	**230**	116	11	357	
1974	15	**248**	**111**		359	359
1975	25	**281**	**96**		377	377
1976	9	162	**111**		273	375
	16	**264**	94	3	361	
1977	16	218	**189**		407	498
	30	**309**	135		444	
1978	15	296	**213**		509	654
	29	**441**	177		618	
1979	14	305	**211**		516	539
	29	**328**	139		467	
1980	5	192	**184**	1	377	387
	12	**203**	145		348	

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[1] Where only one date is listed, peaks for both age classes occurred on same date that year.

Changes in the Numbers of Adult Eagles

During 1977–1980, variation in the number of adults accounted for more of the variation in total numbers than did the variation in number of subadults. During these years, the range of variation was 238 for adults (a maximum of 441 and a minimum of 203) but only 29 for subadults (213 and 184) (Table 4).

Turnover Rates

Higher variation in adult numbers may be related to the adults' shorter stays at the Glacier concentration during years in which salmon are less abundant. This hypothesis is supported by preliminary results from an ongoing study of long-range movement patterns of the McDonald Creek eagles.

During years of comparatively few salmon, subadults remain to feed along McDonald Creek longer than do adults. Subadults, being less skillful at finding prey, remain where there are at least some fish available, if not through direct means, then through kleptoparasitism of (stealing from) other eagles, gulls, or ducks. Subadults (especially birds less than a year old) may tolerate intense competition for food at a given location because they have no experience with food sources farther along the migration route—they do not know of better places to go. In contrast, adults with well-established wintering destinations to which they have been returning for a number of years, tend to move on to areas where they have found better food supplies in the past (Spencer 1976). It would seem to be more efficient, from an energetics standpoint, to move on to a known food source than stay at McDonald Creek and compete for limited food. Therefore, during years of comparatively few salmon, adult Bald Eagles stay for a much shorter duration than during years of salmon abundance. The result is a very high turnover rate and little aggregation of adults when salmon are limited. In contrast, during years of abundant salmon, adult eagles "accumulate" and tend to stay until salmon become less plentiful; thus, early migrating adults (October) are still present on the creek when later migrants (November) arrive.

Although behavioral cues indicating a food source farther south may be transmitted from departing adults to subadults (i.e. from experienced to inexperienced eagles), in the presence of available food subadults may minimize or ignore this information. For subadults, the attraction of remaining with a certain, though inadequate, food source may outweigh the uncertainty of continuing south to an unknown food supply.

We do not believe this scenario to be inconsistent with the early peak in subadult numbers discussed beyond. Because subadults tend to arrive earlier, many have been present at the concentration for several weeks before most adults arrive. After the subadults have fed for several weeks and have a good reserve of stored energy, their "urge" to move south may eventually override the attraction to stay at the site. Finally, all remaining adults and subadults depart rapidly as salmon become scarce in late autumn.

The motivation to stay or depart is influenced by a complex set of variables, the combination of which determines the response. Responses probably differ among age classes, perhaps between sexes, and from year to year as conditions vary.

Other Effects on Numbers

A sudden drop in numbers of adults could be related to attrition of these age classes rather than being an artifact of duration of stay. The adult group could be, and in some instances undoubtedly is, subject to selective mortality—as when mature eagles are killed for the illegal traffic in feathers, talons, etc. (Anon. 1981b). Subadults would probably be stressed at least as strongly as would adults by other possible causes of selective mortality (severe weather, starvation, loss of habitat).

During some years environmental conditions (especially unusual and severe changes in weather patterns and wind directions) may favor southward migration on a route that does not pass close enough to Glacier to allow visitation of the salmon run.

ASYNCHRONY IN ARRIVAL OF ADULTS AND SUBADULTS

In the Midwest, subadult eagles tend to move south earlier than do adults (Sprunt and Ligas 1966). A similar pattern exists in South Dakota, where subadults outnumber adults until the cold winter months (Steenhof 1976). This pattern is less clear in some areas farther west. In Utah (Edwards 1969) and in Washington (Servheen and English 1979, Fitzner and Hanson 1979) the adults seem to arrive first. A study of eagles marked at Besnard Lake, Saskatchewan (Gerrard et al. 1978), suggested that older subadults moved south earlier and migrated farther than did birds not yet a year old.

It may not be accurate to generalize about arrival or departure synchrony in age classes without regard to latitude, longitude, sex, or

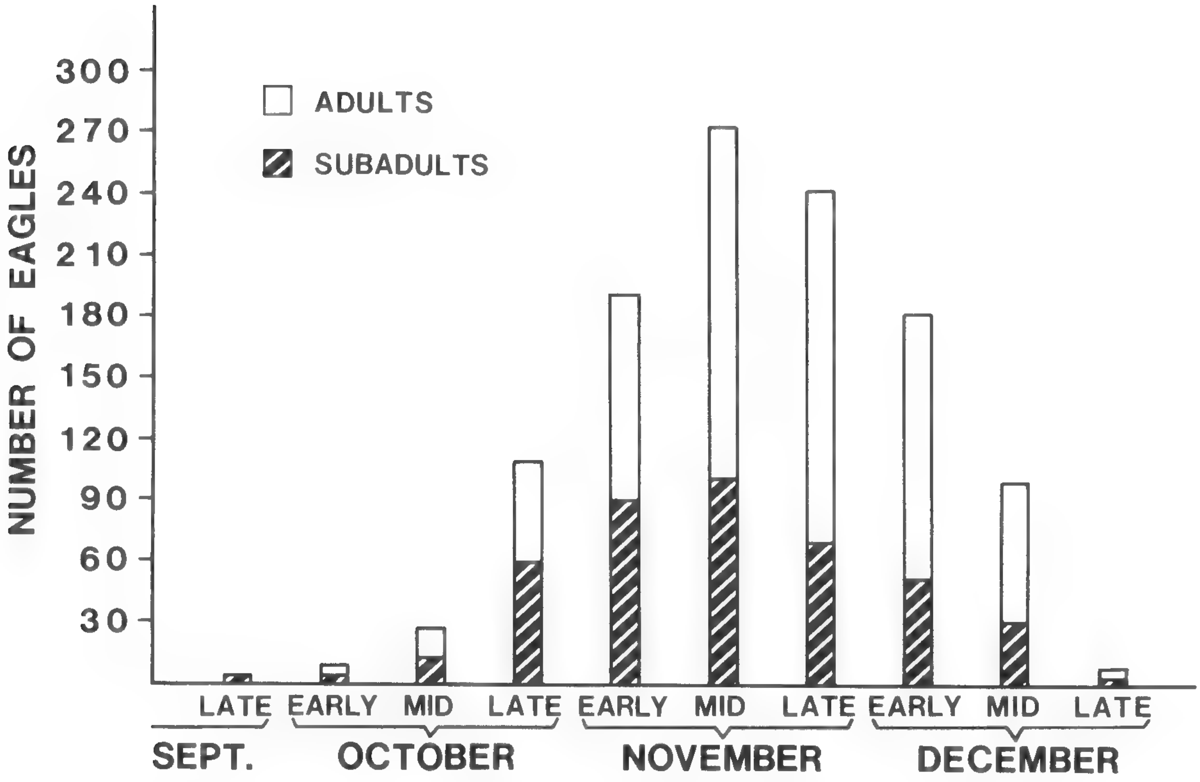

Figure 7. Mean number of adult and subadult Bald Eagles recorded at the Glacier concentration, 1965–1980. Early = 1st to 10th of month, mid = 11th to 20th, late = 21st to end of month.

specific subadult age group. Subadults, especially the youngest age classes, may arrive in some areas before adults, but then lag behind in further movement south. Perhaps an even more basic inaccuracy is the propensity to generalize about persistent patterns in synchrony of age-class movements. These movements may vary from year to year as well as from one part of the continent to another.

In 16 years of counting the Glacier concentration (1965–1980), we found that the number of subadult eagles peaked earlier than did the number of adults in 10 years, and at the same time in the other 6 (Table 4). The mean date for the maximum count of subadults was 14 November; for adults, 20 November; and for the total number, 18 November. Figure 7 illustrates this pattern of count means for the 16 years, and Figure 8 shows the pattern in a representative year (1977). The number of adults at the concentration increased and then decreased more rapidly than did that of the subadults. In the six years that the age classes peaked together, the proportional increase between the peak week and the week before was 50 percent for adults and 30 percent for subadults.

Based on the total numbers of adults and of subadults seen in all counts in all years (1965–1980), the percentage of subadults before 18 November (the mean high count date) was 44.5; after that it dropped to 30.4 percent (Table 5)—a statistically significant difference (Chi-square test, p = 0.05).

ANNUAL CHANGES IN AGE RATIOS

The age ratios observed within a species are not necessarily an accurate indication of the population status of that species unless many

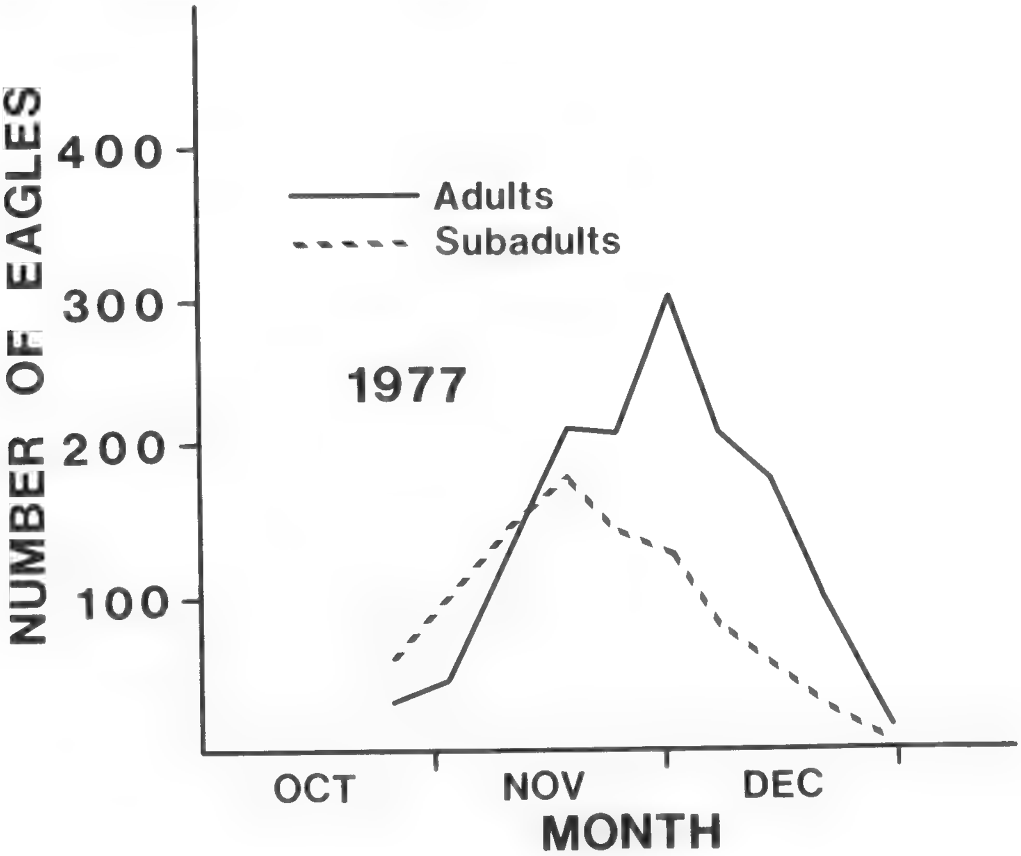

Figure 8. Count totals for autumn 1977, showing the more rapid increase and decrease of adults compared to subadults, and the earlier peak in subadult numbers.

TABLE 5

Total Number of Eagles and Percentage of Subadults Counted Before and After Mean Peak Count Date

Count period	*Adults*	*Subadults*	*Totals*	*% Subadults*
Before 18 November	6412	5149	11561	44.5
After 18 November	7612	3324	10936	30.4
Totals	14024	8473	22497	37.7

other variables (such as mortality rates) are taken into consideration (Grier 1979). At present, collateral evidence for Bald Eagles is insufficient to allow the use of age-ratio data alone to determine population changes. The proportion of subadult eagles in any given group also may not indicate any real population information because many areas are not equally attractive to adults and subadults (Southern 1963, Newton 1979). However, because Glacier is a stopping point along a migration route rather than a wintering area, long-term trends in ratios of age groups may serve as a rough index of age-class stability in this group of eagles.

The percentage of subadults counted at Glacier varied from 25 to 56 percent, depending on the year and the calculation method used (Table 6). The percentage varied considerably both within a given season (from 2 to 11 percentage points per year within the 3 types of calculation) and annually (from 27 to 29 points per calculation method within the 16-year period). If the turnover rate and time of peak counts differ between the two age groups, as they do in Glacier, calculation of the entire season's data (Table 6, Column 3) is the most meaningful. Based on this method of calculation, the percentage of subadults present in the second half of the study (1973–1980) was significantly decreased (Chi-square, $p = 0.05$) compared with that in 1965–1972.

A continuing trend of change in the count ratios at Glacier—suggesting a current decrease in Bald Eagle reproduction or subadult survival — may indicate a true change in age-class ratios in the populations from which these migrating eagles come. This information, however, should be used with caution (Grier 1979). In hypothetical life-table models Grier (1980) showed that changes in age ratios may give little-or-no indication of actual population changes, at least over periods up to 15 years. This further emphasizes the need for long-term monitoring of ratios and for avoiding premature conclusions.

SUMMARY

The natural feeding regimes of Bald Eagles in northwestern North America have been altered in many ways by human activities. In the Columbia River system, dams have eliminated more than half of the spawning habitat originally available to native Pacific salmon, upon which eagles have fed for centuries. Human disturbance and water pollution have also driven eagles from many other areas. In contrast, spawning runs of introduced Kokanee Salmon in several land-locked waterways in the Northwest have attracted increasing numbers of migrating eagles where human disturbance is minimal.

TABLE 6

Percentage of Subadult Bald Eagles in the Glacier National Park Concentration, 1965–1980

Year	*High*[1] *total count*	*High*[2] *individual count*	*Total*[3] *individual count*
1965	37	37	42
1966	33	37	39
1967	28	33	39
1968	36	36	34
1969	32	32	36
1970	32	35	41
1971	54	52	56
1972	33	33	35
1973	34	43	39
1974	31	31	27
1975	25	25	32
1976	26	30	31
1977	30	38	39
1978	29	33	36
1979	41	41	39
1980	49	48	40
Mean	34.2	35.7	37.7

[1] % Subadults based on day of maximum total count.

[2] % Subadults based on highest count of adults and highest count of subadults even though maxima may have occurred on different dates.

[3] % Subadults based on total adults and total subadults counted during entire autumn.

The concentration in Glacier National Park, Montana, grew from 37 Bald Eagles in 1939 to 618 in 1978—probably the greatest single concentration in the conterminous 48 states. The eagles at Glacier were counted along a standardized route weekly during the autumns of 1965–1980. About 90 percent of the eagles observed were along the 4-km (2.5-mi) stretch of lower McDonald Creek. Food (Kokanee Salmon) is the foundation of the Glacier eagle concentration. Birds stay along McDonald Creek until salmon are no longer available (October-December); southward migration then resumes.

Initial discovery of the salmon run by eagles probably occurred through chance or local searching during migration. As the number of eagles grew, long-distance sight detection of group soaring over McDonald Creek became more likely. Raptor visual acuity is greater than that of humans and may allow eagles to locate other eagles soaring over abundant food supplies more than 23 km (14 mi) away. Discovery of the salmon also may have occurred through simple following of other eagles or through information transfer at roosts.

In recent years, variations in total numbers of eagles at the concentration have resulted from changes in abundance of salmon and from reduced human disturbance along McDonald Creek.

Eagle use days were calculated using numbers of eagles counted and the length of time eagles (not necessarily the same ones) were present at the concentration. Based on an estimated requirement of 500 g (17.5 oz) of salmon per day for body maintenance of eagles, in the peak year of 1978 about 45,800 salmon would have been required to sustain the eagles present at Glacier. This number exceeds the estimated spawning population of salmon in the entire creek in most recent years—45,400 in 1980, when approximately 16,400 would have been consumed by eagles, just for maintenance. During the period of greatest abundance of salmon carcasses, however, many eagles consume more than their energy maintenance level and thus build energy reserves before continuing the migration. The maximum number of eagles that can be supported at this concentration probably is now limited by food.

Changes during 1977–1980 have reflected much greater variation in the numbers of adults than in subadults. This may best be explained by a widely varying turnover rate for adults, and perhaps also by selective mortality or shifts in migration routes.

The high counts for adults and subadults are asynchronous in 10 of the past 16 years. The mean dates of peak counts are 14, 20, and 18 November, respectively, for subadults, adults, and the total number of eagles. The percentage of subadults in the eagles counted at the concentration has shown a significant reduction (40 to 36 percent) when the first eight years of the study (1965–1972) are compared with the most recent eight years (1973–1980).

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B. R. McClelland and L. S. Young:
SCHOOL OF FORESTRY
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D. S. Shea,[1] *P. T. McClelland, H. L. Allen,*[2] *and E. B. Spettigue:*[3]
UNITED STATES DEPARTMENT OF THE INTERIOR
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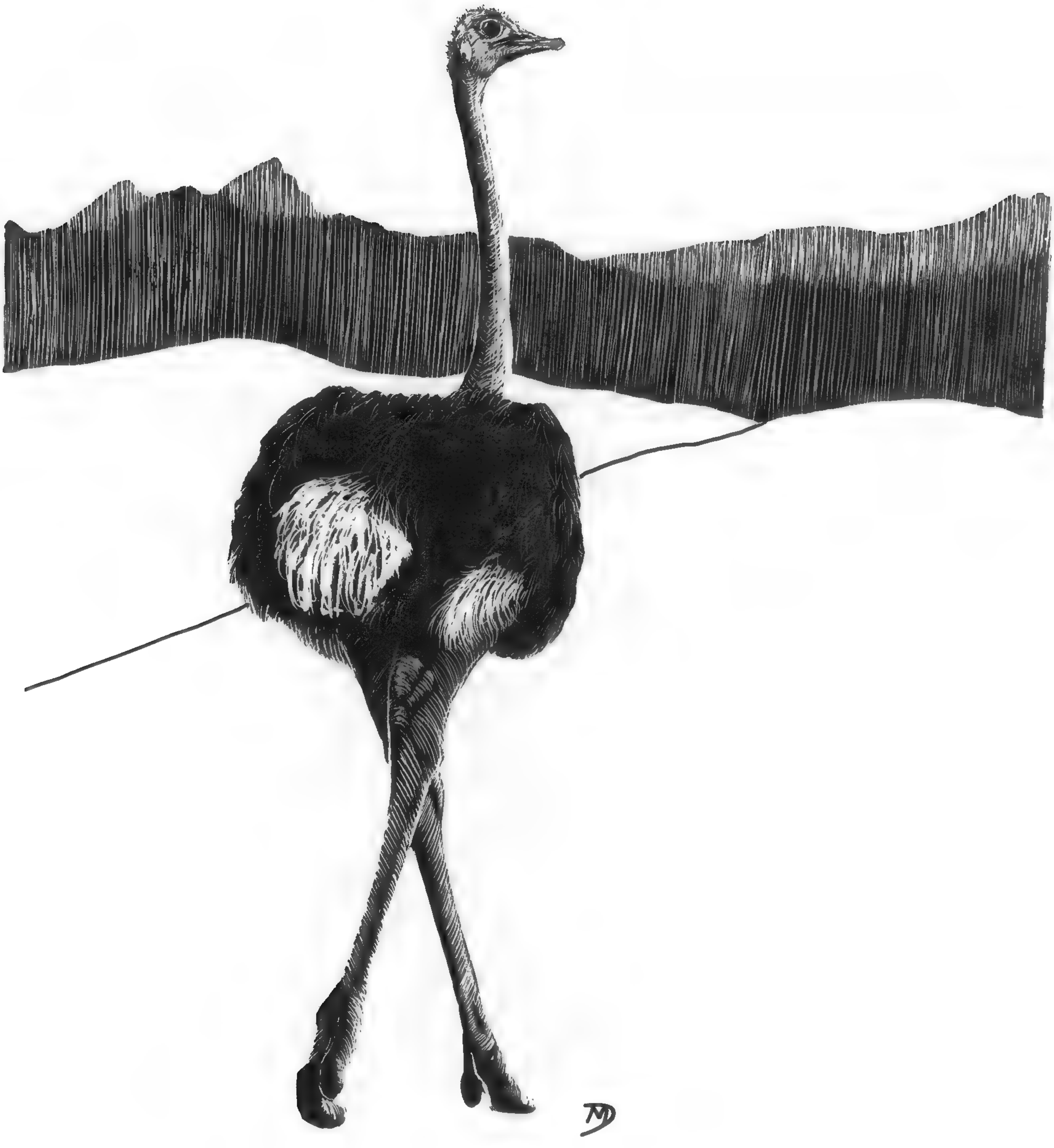
Bald Eagle, *Haliaeetus leucocephalus.* Drawing by Patrick J. Lynch, courtesy of the artist.



Ostrich, *Struthio camelus.* Scratchboard by David S. Maehr.

Kittiwake Greeting. Painting of Black-legged Kittiwake (*Rissa tridactyla*) by Robert Bateman. Courtesy of Mill Pond Press, Inc. and the artist.

AUTHORS AND ARTISTS BRIEFLY NOTED

HARRIET ALLEN is a research biologist with the Washington Department of Game and is now stationed in Seattle.

JOHN ANDERTON is an undergraduate student of art and biology at the University of Pittsburgh in Pennsylvania.

ROBERT BATEMAN is a Canadian wildlife artist who makes his home in Milton, Ontario.

JOSEPH BELL is the recently-retired Curator of Birds at the New York Zoological Park, Bronx.

GUY DANELLA is a free lance artist who works from his studio in Utica, New York.

ROBERT DICKERMAN is a professional ornithologist and a member of the Microbiology faculty at Cornell University Medical College in New York.

RICHARD FFRENCH has taught languages, history, and music in Trinidad since 1958; he *says* he studies birds in his spare time.

JOHN FITZPATRICK is Associate Curator and Head of the Division of Birds at Field Museum of Natural History, Chicago.

DANA GARDNER is staff artist for the Western Foundation of Vertebrate Zoology, Los Angeles.

GEORGE GILBERT is a free lance artist who lives in Stanardsville, Virginia.

ANDRES JOHNSON is at the Fundación Vida Silvestre Argentina in Buenos Aires.

CAMERON KEPLER is a Research Biologist for the U.S. Fish and Wildlife Service, Endangered Wildlife Research Program.

WARREN KING is President of the U.S. Section of the International Council for Bird Preservation.

PAT LYNCH is a student at the Department of Medical Illustration, Yale University, New Haven, Connecticut.

DAVID MAEHR is a Research Biologist at the Florida Game and Fresh Water Fish Commission in Gainesville, as well as a free lance wildlife artist.

B. RILEY MCCLELLAND is an Associate Professor at the School of Forestry, University of Montana, Missoula, and a research biologist with the National Park Service in Glacier National Park, Montana.

PATRICIA MCCLELLAND has been a research associate with the Glacier Bald Eagle project since 1965; she resides in West Glacier, Montana.

GARY NUECHTERLEIN is a Lecturer at the Museum of Zoology, University of Michigan, Ann Arbor.

JOHN O'NEILL is an ornithologist and bird artist, and Director of the Museum of Zoology, Louisiana State University, Baton Rouge.

KENNETH PARKES is Curator of Birds and Chief Curator of Life Sciences at Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

DIANE PIERCE is a free lance bird artist who works out of her new studio, "Edge of the Wild," in Bonita Springs, Florida.

H. DOUGLAS PRATT is a professional artist and ornithologist, and a Research Associate of the Museum of Zoology, Louisiana State University, Baton Rouge.

LLOYD SANDFORD (deceased) served as an artist for the New York Zoological Society.

DAVID SHEA is a former Glacier National Park biologist and ranger; he now lives in Powers, Oregon.

NOEL SNYDER is a Research Biologist for the U.S. Fish and Wildlife Service, Endangered Wildlife Research Program, currently assigned to the California Condor research team.

ELIZABETH SPETTIGUE is a student in Wildlife Ecology and Communication at Montana State University, Bozeman.

ROBERT STORER is Curator of Birds and Acting Director of the Museum of Zoology, University of Michigan, Ann Arbor.

GEORGE MIKSCH SUTTON is an artist, author, and lecturer as well as George Lynn Cross Research Professor of Zoology Emeritus at the University of Oklahoma, Norman.

MELVIN TRAYLOR is Curator Emeritus in the Department of Zoology at Field Museum of Natural History, Chicago.

LEONARD YOUNG is a graduate student in Wildlife Biology at the University of Montana, Missoula.

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Grasshopper Sparrow, *Ammodramus savannarum*. Drawing by Patrick J. Lynch, courtesy of the artist.

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Although *The Living Bird* will suspend publication with this (19th) issue, in order to use the Laboratory's resources for *The Living Bird Quarterly,* it is hoped that *The Living Bird* in its traditional format will resume publication in the future, probably as an occasional journal rather than as an annual.

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The Cornell Laboratory of Ornithology is a center for the study and cultural appreciation of birds, with headquarters in Sapsucker Woods, three miles from the main campus of Cornell University in Ithaca, New York. The Laboratory is open seven days a week and visitors are welcome.

The Laboratory is primarily concerned with scientific, educational, and cultural activities. Among its scientific pursuits are the Peregrine Falcon Re-Introduction Program, the Library of Natural Sounds, and the Cooperative Research Program (administered in conjunction with the National Audubon Society). The pigeon orientation studies, begun by the late Cornell professor, William T. Keeton, are now under the auspices of the Laboratory. Please write to the Laboratory for information on these programs and how you can help contribute to their success.

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Phoenix (American subspecies of the Egyptian-Arabian form). Drawing by Guy Danella.

EDITOR'S NOTE: Because this issue of *The Living Bird* was edited at The Florida State Museum, University of Florida, Gainesville, warm thanks are due to the administration, faculty, and students of that institution for support and assistance of many kinds. I am also grateful to the Editorial Board of the journal, to colleagues around the country who refereed manuscripts, and to Oliver L. Austin, Jr., and J. William Hardy for their editorial advice. Very special thanks go to Alice W. Cullu, my volunteer editorial assistant, who read all the edited manuscripts with great care for clarity of expression and who made sure that none of us broke that most serious of the Ten Commandments for Technical Writers: Thou shalt not cloud thy message with a miasma of technical jargon.—*Mary H. Clench.*

ERRATA: *The Living Bird,* Eighteenth Annual (1979–1980)

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p. 26: for Saw Whet Owl, *Aegolius acadicus, read* Pygmy Owl, *Glaucidium gnoma.*

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for Yunlun *read* Yunlin

p. 191, text: for warm temperature *read* warm temperate

p. 192, figure caption: for 1947 *read* 1957
for Shao Lai (2) *read* Hsueh (2)
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for Chen Chung (5) *read* Hsin Chang (5)
for Hohuan (6) *read* Tawu (6)

p. 199: Figure 5 is printed backwards

p. 209: for Wang, C. k'U. *read* Wang, C. K.

p. 215: *add* to the staff list, Charles R. Smith, Director of Public Education.